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"JÚLIO DE MESQUITA FILHO"
INSTITUTO DE BIOCIÊNCIAS – RIO CLARO

PROGRAMA DE PÓS-GRADUAÇÃO EM CIÊNCIAS BIOLÓGICAS (ZOOLOGIA)

A HISTÓRIA NATURAL AUXILIANDO A ESCOLHA DAS VARIÁVEIS PREDITORAS DOS MODELOS DE DISTRIBUIÇÃO DE ESPÉCIES: PROTOCOLOS E SUBSÍDIOS PARA OS PLANOS DE CONSERVAÇÃO DOS ANFÍBIOS

JOÃO GABRIEL RIBEIRO GIOVANELLI

Tese apresentada ao Instituto de Biociências do Câmpus de Rio Claro, Universidade Estadual Paulista, como parte dos requisitos para obtenção do título doutor em Ciências Biológicas (Zoologia).

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CERTIFICADO DE APROVAÇÃO

TÍTULO DA TESE: A história natural auxiliando a escolha das variáveis preditoras dos modelos de distribuição de espécies: protocolos e subsídios para os planos de conservação dos anfíbios

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"Nós criamos uma civilização global em que os elementos mais cruciais – o transporte, as comunicações e todas as outras indústrias, a agricultura, a medicina, a educação, o entretenimento, a proteção ao meio ambiente e até a importante instituição democrática do voto – dependem profundamente da ciência e da tecnologia. Também criamos uma ordem em que quase ninguém compreende a ciência e a tecnologia. É uma receita para o desastre. Podemos escapar ilesos por algum tempo, porém mais cedo ou mais tarde essa mistura inflamável de ignorância e poder vai explodir na nossa cara."

O Mundo Assombrado pelos Demônios: A Ciência Vista como uma Vela no Escuro

Carl Sagan, 1995

Resumo Geral

Na última década houve um grande desenvolvimento nos Modelos de Distribuição de Espécies (MDE), com diversas aplicações na conservação da biodiversidade. No entanto, apesar dos avanços recentes, a seleção de variáveis preditoras tem sido relativamente negligenciada na construção dos MDE. Este procedimento deveria ser um dos passos cruciais do processo de modelagem, já que as variáveis preditoras estão relacionadas diretamente à capacidade dos modelos de capturar os requisitos ambientais das espécies. Neste contexto, os anfíbios são excelentes organismos modelo para avaliar a importância da seleção de variáveis preditoras ecologicamente significativas no MDE. Isto pode trazer avanços para a biogeografia e biologia da conservação, uma vez que os anfíbios são usados como bioindicadores da qualidade ambiental e da integridade de hábitat. A presente tese de doutorado teve como objetivo principal verificar o efeito da utilização de variáveis preditoras ecologicamente significativas no processo de modelagem dos anfíbios e posteriormente aplicar parte deste conhecimento na comunidade de anfíbios do Estado de São Paulo, visando verificar o potencial desta metodologia para identificar áreas de alto valor de riqueza de anfíbios e verificar também o potencial de invasão de *Eleutherodactylus jonhstonei*, uma espécie de anfíbio invasora registrada para o Estado de São Paulo. No primeiro capítulo avaliamos a importância da seleção de variáveis essenciais ao MDE usando os anfíbios como estudo de caso. O segundo trata especificamente do protocolo de modelagem dos anfíbios do estado de São Paulo. O foco central deste capítulo foi examinar se os dados biológicos existentes para o estado são eficientes para gerar subsídios para os planos de conservação. Finalmente, o terceiro capítulo é sobre a modelagem do potencial de invasão de *Eleutherodactylus johnstonei* no Brasil.

Palavras-chaves: Anfíbios, História natural, Invasão biológica, Modelos de distribuição de espécies, Planos de conservação, Sensoriamento remoto e Variáveis preditoras.

General Abstract

In the last decade there has been a great development in the Species Distribution Models (SDM), with several applications in conservation planning. However, despite recent advances, the selection of predictor variables has been relatively neglected in the construction of SDM. This methodological approach should be one of the critical steps of the modeling process, as the predictor variables are directly related to the ability of models to capture the environmental requirements of the species. In this context, amphibians are excellent model for assessing the importance of selecting ecologically meaningful variables in the SDM. This methodology may lead to advances in biogeography and conservation biology, since amphibians are used as bioindicators of environmental quality and habitat integrity. The aim of the work was to verify the effect of the use of ecologically meaningful variables in the amphibian modeling process and to apply part of this knowledge to the amphibian community of São Paulo state, checking the potential of this methodology to identify areas of high amphibian richness value and to verify the potential invasion of *Eleutherodactylus jonhstonei*, an invasive amphibian species registered in São Paulo state. In the first chapter we evaluated the importance of selecting essential variables in SDM using amphibians as a case study. The second chapter deals specifically with the amphibian modeling protocol of São Paulo state. The central focus of this chapter has been to examine whether existing biological data for the state is efficient in generating subsidies for conservation plans. Finally, the third chapter is about modeling the potential of *Eleutherodactylus johnstonei* invasion in Brazil.

Keywords: Amphibians, Natural history, Biological invasion, Species distribution models, Conservation planning, Remote sensing, and Predictor variables.

Sumário

INTRODUÇÃO GERAL

Na última década houve um grande desenvolvimento dos modelos de distribuição de espécies (MDE) (e.g. GUISAN; THUILLER, 2005; ELITH et al., 2006; DINIZ-FILHO et al., 2009; SOBERÓN; NAKAMURA, 2009). Devido à sua capacidade de associar matematicamente as ocorrências das espécies com conjuntos de variáveis ambientais, os MDE constituiram-se como uma importante ferramenta para subsidiar o planejamento da conservação, principalmente planos de (i) manejo de espécies exóticas, (ii) seleção de hábitats críticos, (iii) seleção de áreas prioritárias para conservação e (iv) translocações de fauna (e.g. GUISAN et al., 2013; URBINA-CARDONA et al., 2019).

No entanto, apesar dos grandes avanços dos MDE para a conservação da biodiversidade, o uso indiscriminado dos modelos - que muitas vezes não utilizam uma seleção criteriosa das variáveis de resposta (pontos de ocorrência) e variáveis preditoras (camadas ambientais) - podem produzir modelos não acurados (MORALES et al., 2017). Os MDE tendenciosos podem não causar problemas significativos quando aplicados em estudos teóricos em pequena escala (resolução grosseira) (GUISAN et al., 2007). Porém, podem ser problemáticos em estudos que objetivem subsidiar ações de conservação, gerando diversos custos ecológicos e econômicos (GUISAN et al., 2013).

Basicamente, a construção de um MDE se baseia em um processo de três etapas: i) compilação e seleção de dados de entrada (variáveis de resposta e preditoras), ii) escolha dos algoritmos e iii) predição espacial. Neste processo houve avanços na compilação das variáveis de resposta, com diversas ferramentas baseadas na prevenção e correção dos dados de ocorrência, com o intuito de selecionar somente informações de qualidade para os modelos (CHAPMAN, 2005). Outro avanço considerável foi o desenvolvimento de diversos algoritmos de modelagem que já foram amplamente testados, mostrando-se aptos para modelar a distribuição das espécies (e.g. STOCKWELL; PETERS, 1999; HIJMANS et al.,

2002; MUNHÕZ et al., 2009; PHILLIPS et al., 2006). Além disso, metodologias baseadas no consenso de diferentes métodos de modelagem podem fornecer uma estrutura para lidar com as incertezas de predição inerentes a cada modelo separadamente (DINIZ-FILHO et al., 2009).

Apesar destes últimos avanços recentes, a seleção de variáveis preditoras tem sido relativamente negligenciada na construção dos MDE. A seleção de variáveis preditoras é um dos passos cruciais do processo de modelagem, já que está relacionada diretamente à capacidade dos modelos em capturar os requisitos ambientais das espécies. Neste sentido, era de se esperar uma preocupação maior no processo de seleção de variáveis ecologicamente significativas nos modelos (MOD et al., 2016). Um dos métodos mais comumente utilizados é a seleção de variáveis preditoras não autocorrelacionadas (ou seja, camadas ambientais não redundantes) (e.g. AUSTIN, 2007; AUSTIN; VAN NIEL, 2011; MOD et al., 2016). No entanto, mesmo selecionando corretamente as variáveis, o método de construção da variável preditora também pode influenciar os resultados dos modelos (e.g., WILSON; JETZ, 2016; MARIA; UDO, 2017). A maioria das variáveis preditoras amplamente utilizadas é baseada em interpolações de dados espaciais adquiridos no solo através de estações de monitoramento (e.g., WorldClim versão 1.4; HIJMANS et al., 2005). Este tipo de informação pode não refletir a heterogeneidade espacial presente na distribuição geográfica das espécies, especialmente aquelas com distribuição restrita (MCLAUGHLIN et al., 2017) ou com distribuição geográfica contemplando paisagens antropizadas, principalmente espécies exóticas (GALLARDO et al., 2015). Porém, estudos recentes mostram que a inclusão de novos preditores, baseados, por exemplo, em produtos derivados de sensoriamento remoto, podem melhorar o desempenho do modelo (e.g., HE et al., 2015; TUANMU; JETZ, 2015; WILSON; JETZ, 2016).

Nesse contexto, o entendimento da história natural das espécies pode auxiliar na escolha das variáveis preditoras, incluindo nos MDE varíaveis ecologicamente sisgnificativas para as espécies em questão. Os anfíbios são excelentes organismos modelo para avaliar a importância da seleção de variáveis preditoras essenciais no MDE. Os anfíbios são animais ecologicamente especializados, com baixa capacidade de dispersão e alta sensibilidade a mudanças ambientais, o que torna o MDE uma importante ferramenta para este grupo (GIOVANELLI et al., 2010). Este táxon é um dos mais diversos e ameaçados vertebrados do mundo, com aproximadamente 8.040 espécies conhecidas (FROST, 2019), das quais cerca de 1.900 estão ameaçadas (AMPHIBIAWEB, 2018). Desta maneira, investigar as variáveis ecologicamente significativas para modelar esse grupo pode trazer benefícios para todas as áreas da biogeografia e biologia da conservação, uma vez que os anfíbios são usados como bioindicadores da qualidade ambiental e da integridade de hábitat (e.g., WELSH JR.; OLLIVIER, 1998; GARDNER et al., 2007).

A presente tese de doutorado surgiu da necessidade de criar protocolos de MDE de anfíbios mais acurados para serem aplicados em demandas de planejamento ambiental, tendo como objetivo principal verificar o efeito da utilização de variáveis preditoras ecologicamente significativas para os anfíbios nos MDE e posterior aplicar parte deste conhecimento na comunidade de anfíbios do Estado de São Paulo, visando verificar o potencial desta metodologia para identificar áreas de alto valor de riqueza de anfíbios e verificar também o potencial de invasão de *Eleutherodactylus jonhstonei*, uma espécie de anfíbio invasora registrada para o estado.

Após o advento do Programa Biota-FAPESP, que apoiou projetos de prospecção da biodiversidade no Estado de São Paulo, bem como a sistematização desta informação em um banco de dados de amplo acesso (http://sinbiota.cria.org.br), houve uma intensificação do conhecimento da biodiversidade paulista. Neste contexto, se destaca o grupo dos anfíbios que

experimentou um incremento da ordem de 31% em relação ao número de espécies registradas para o Estado em 1998. Além disso, o número de espécies registradas representa 27% da riqueza de espécies do país, demonstrando também que o estado é a região brasileira onde os anfíbios foram mais estudados (ROSSA-FERES et al., 2011). Neste contexto, desenvolver ferramentas que possibilitem estimar a potencial riqueza de anfíbios através de dados de qualidade, acumulados nas bases de dados, pode ser útil para gerar diagnósticos mais precisos que podem ser utilizados como subsídio na caracterização da fauna em áreas de influência de empreendimentos, auxiliar no planejamento do zoneamento de Unidades de Conservação e no zoneamento territorial ambiental do Estado de São Paulo.

No total, a tese possui três capítulos já em formatos de artigos para serem submetidos para periódicos científicos da área. O primeiro deles surgiu da necessidade de criar protocolos de MDE de anfíbios mais robustos e que atendam demandas de conservação. Para isso, avaliamos a importância da seleção de variáveis essenciais em MDE usando os anfíbios como estudo de caso. Através de compilação de literatura, investigamos as variáveis preditoras usadas em modelos de distribuição de anfíbios, verificando se esses preditores correspondem aos requisitos ecológicos das espécies. Verificamos que existe uma tendência do uso massivo de variáveis relacionadas à temperatura e a água, sendo o uso de variáveis relacionadas às características bióticas e fisiográficas dos habitats ocupados por anfíbios ainda pouco exploradas. No final, usando dois estudos de caso, demonstramos o efeito de incluir variáveis essenciais para os modelos de distribuição de anfíbios.

O segundo capítulo trata especificamente do protocolo de modelagem dos anfíbios do estado de São Paulo. O foco central deste estudo foi examinar se os dados biológicos existentes para o estado de São Paulo são eficientes para identificar áreas de alto valor de diversidade de anfíbios e detectar lacunas na representação de espécies dentro das Unidades de Conservação. Primeiro, propusemos uma metodologia para modelar as distribuições

geográficas de anfíbios em escala fina usando variáveis preditoras essenciais que correspondem aos requisitos de nicho ecológico conhecidos das espécies. Em um segundo momento, usamos a metodologia de empilhamento de modelos (do inglês S-SDMs), combinando MDEs com os *thresholds* mais utilizados atualmente nos modelos de presença. Após isso, comparamos os resultados em termos da riqueza com informações reais fornecidas pelo ATLANTIC AMPHIBIANS: um conjunto de dados de comunidades de anfíbios da Mata Atlântica (VANCINE et al., 2018).

Finalmente, o terceiro capítulo é sobre a modelagem do potencial de invasão de *Eleutherodactylus johnstonei* no estado de São Paulo. Neste capítulo apresentamos um protocolo de modelagem para prever a distribuição potencial dessa espécie invasora, verificando se existem áreas adequadas para a espécie no bioma Mata Atlântica. Para isso, usamos o algoritmo MAXENT (i) para modelar a distribuição geográfica nativa dessa espécie e (ii) projetar esse modelo para todo o Brasil. Além disso, usamos variáveis preditoras derivadas de sensoriamento remoto visando melhorar o desempenho dos modelos, principalmente em escalas regionais.

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Capítulo 1

Natural history supports the choice of ecologically meaningful variables in amphibian distribution models: an extensive review and case studies

RESEARCH REVIEW

Natural history supports the choice of ecologically meaningful variables in amphibian distribution models: an extensive review and cases studies

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Abstract

Species distribution models (SDM) have been one of the most relevant techniques to understand the patterns of species distribution. Despite the great advances that the SDM have brought for conservation biology, it is also of concern the indiscriminate use of the SDM in default automatic conceptualization and building. Here, we evaluate the importance of the selection of ecologically meaningful variables in SDM using amphibians as study case. Through a survey in the peer reviewed literature, we investigated the predictor variables used in amphibian distribution models, verifying if these predictors correspond to the known ecological niche requirements of amphibian species. We found that there is a tendency of the massive use of temperature- and water-related variables, but the use of variables related to the biotic and physiographic characteristics of the habitats occupied by amphibians is still little explored. Using two case studies, we fit models and interpret them, demonstrating the effect of including ecologically meaningful variables for the amphibian distribution models. Considering that model prediction errors can lead to environmental and economic costs, we encourage researchers to select and insert new variables into their models, which may help in the generation of robust models for amphibian conservation projects. So, we show a series of solutions for modelers to help improve the accuracy of their predictions.

Keywords: Amphibians, Bioclimatic variables, Natural history, Predictor variables, Remote sensing data, Species distribution models.

INTRODUCTION

Due to its ability to statistically associate the presence of a species with a set of environmental variables, species distribution models (SDM) have been one of the most relevant techniques to understand the patterns of species distribution (e.g., Guisan & Thuiller 2005, Araújo & New 2007, Elith & Leathwick 2009, Guisan et al. 2017). These features have made SDM one of the most popular tools in conservation biology, being useful in generating spatial explicit data that can support the selection of protected areas, identification of critical habitats, and predict biological invasions (Guisan et al. 2013).

Currently, there are several methodologies to select and to evaluate the models (e.g., Carpenter et al. 1993, Guisan & Thuiller 2005, Elith & Graham 2006, Araujo & New 2007, Zimmermann et al. 2010, Elith et al. 2011, Booth et al. 2014, Qiao et al. 2015). In addition, there is concern about the quality of response variable (i.e., species occurrence data), mainly those available in biological collections and museums (e.g., Graham et al. 2004, Chapman 2005, Beck et al. 2014). However, despite the great advances of the SDM for conservation biology, it is also of concern the indiscriminate use of the SDM in default automatic configuration, which can produce non-optimal models (Morales et al. 2017). Biased SDM may not cause problems when applied in theoretical studies in coarse resolution (Guisan et al. 2007), but non-optimal models can be problematic in fine-resolution studies to subsidize conservation decisions. These errors can generate diverse ecological and economic costs (Guisan et al. 2013).

One of the ways to develop more accurate models is to select the most appropriate predictor variables, especially those not cross- correlated (i.e. redundant environmental layers) (e.g., Austin 2007, Austin et al. 2011, Mod et al. 2016). There are several techniques that assist in this choice (i.e. correlation, factorial, variance inflation factor, PCA analyses) (e.g., Giovanelli et al. 2010, Pradhan 2016, Petitpierre et al. 2017). However, even using the most

appropriate predictor variables they may not influence the physiology, behavior, and other biological factors of the species. Moreover, even if we correctly select the variables, the method of building the predictor variable (derived of interpolated data or remote sensing) may also influence the results of the models (e.g., Wilson & Jetz 2016, Maria & Udo 2017). Most of the currently widely used variables are based on interpolations of spatial data acquired on the ground through monitoring stations (e.g., Worldclim version 1; Hijmans et al. 2005), that often do not reflect the spatial heterogeneity of the geographic distribution of the species, especially those with restricted distribution (i.e., microendemic species) (Mclaughlin et al. 2017) or with geographic distribution including anthropic landscapes, mainly exotic species (Gallardo et al. 2015). However, recent studies show that the inclusion of new predictors, based, for example, on remote sensing technologies, may improve model performance (e.g., He et al. 2015, Tuanmu & Jetz 2015, Wilson & Jetz 2016).

In this sense, the first step to subsidize the choice of predictors should be the knowledge of the natural history of the organism in question. A recent study by Fourcade et al. (2017) reinforced this concern modeling 509 European species using pseudo-predictors derived from classical paintings or using a real set of climatic and topographic predictors. The results showed that most models computed from pseudo-predictors were classified as good and sometimes were even better evaluated than models computed using real environmental variables, evidencing the importance of variable selection and the inability of current evaluation metrics to assess the biological significance of distribution models.

Amphibians are excellent model organisms for evaluate the importance of the selection of essential variables in SDM. The amphibians are ecologically specialized animals with low dispersion capacity and high sensitivity to environmental changes, which makes interesting the SDM for this group (Giovanelli et al. 2010). The most common life cycle, based on larval aquatic phase in early life and post-metamorphic terrestrial life, has

implications for the choice of environmental variables relevant to modeling. This taxon is one of the most diverse and endangered vertebrates of the world, with approximately 7,900 known species (Frost 2018), of which around 1,900 are threatened (AmphibiaWeb 2018). In this sense, investigating the ecologically meaningful variables for modeling this group can bring benefits to all areas of biogeography and conservation biology, since amphibians are used as bioindicators of environmental quality (e.g., Welsh Jr. & Ollivier 1998, Gardner et al. 2006).

Here, we investigate in the peer reviewed literature which predictor variables have been used in amphibian distribution models and used two case studies to illustrate the effects of choice of these predictors. It is known that the quality of presence data, choice of algorithms, and evaluation metrics are essential for generating suitable predictive distribution models (e.g. Araujo & Guisan 2006, Elith et al. 2006, Rangel & Loyola 2012). We emphasize here the evaluation for selecting suitable predictor variables, which is sometimes neglected and misused by the choice of predictors not effectively linked to specific physiological/behavioral aspects of a given species. Our primary focus was to examine whether the predictor variables used in amphibian SDM studies are ecologically meaningful for amphibian species. Then, based on the natural history of amphibians, we propose a series of solutions for modelers to help improve the accuracy of their models by guiding them to select appropriate predictors for their SDMs.

NATURAL HISTORY OF AMPHIBIANS: WHAT SHOULD WE KNOW BEFORE PERFORMING SDMs?

Amphibians are derived from lineages of the first terrestrial vertebrates that emerged in the Devonian Period. Despite their long evolutionary history, these animals are still very dependent on aquatic environments for their survival and reproduction (Haddad et al. 2013). The fact that they are ectothermic animals and have permeable skin make this group more susceptible to the conditions and fluctuations of the environment than any other tetrapod (Duellmann & Trueb 1986, Crump 2010). To reduce water loss, amphibians generally rest during the day and avoid the sun and high temperatures, being active mainly after the sunset (Haddad et al. 2013). However, some species from strictly forested environments can forage and reproduce during the day due to the high humidity and low sunlight under the forest canopy. In addition to the behavioral characteristics, there are physiological strategies used by terrestrial amphibians to avoid water loss. Terrestrial amphibians excrete urea and some anuran species can produce uric acid, increasing tolerance to long periods of exposure to dry air (Loveridge 1976, Shoemaker et al. 1972). Another relevant strategy is that amphibians can do skin rehydration in free water or by substrate moisture (Duellmann & Trueb 1986).

Water also has a very significant role in the distribution and ecology of amphibians. Water availability in the environments is a key element in the reproduction of amphibians. Fertilization is generally external and eggs are deposited in the water; then, eggs develop in larvae that complete their aquatic development until metamorphosis. However, not all species have aquatic larvae. Many amphibians can reproduce on land, rocks, trees, or in bromeliads (Haddad & Prado 2005), but these environments must have enough moisture to support the development of the embryos (Figure 1). Furthermore, water seems to be a primary determinant of amphibian species diversity (Hillman et al. 2009). For example, there is a

strong positive correlation between precipitation and amphibian diversity (Zhao et al. 2006, Buckley & Jetz 2007, Vasconcelos et al. 2010).

Considering that, it is a consensus that water and temperature are ecologically meaninful predictors to be used for distribution modeling. However, these environmental variables are a subset of factors that integrate the ecological niche of amphibians. Depending on the geographic scale, factors such as biotic interactions and mobility also delimit the geographic space to be occupied by the species (e.g., Soberón & Nakamura 2009). The reproductive mode is a central aspect of amphibian life history that refers to specificities in the oviposition and tadpole developmental sites, among other traits (Haddad & Prado 2005). These specificities generate results in different modes of reproduction that depend on numerous environmental peculiarities. The anuran amphibians stand out with 40 currently recognized reproductive modes (Haddad & Prado 2005, Iskandar et al. 2014, Crump 2015). These modes vary from the simplest (i.e. deposition of eggs directly in the water) to more complex ones (i.e. direct development and viviparity) (Haddad et al. 2013). Thus, it is possible to increase the efficiency of distribution models by considering the predictor variables that influence the reproductive contexts of amphibians (e.g., streams, swamps, soil moisture, and vegetation) (e.g., Vasconcelos et al. 2017).

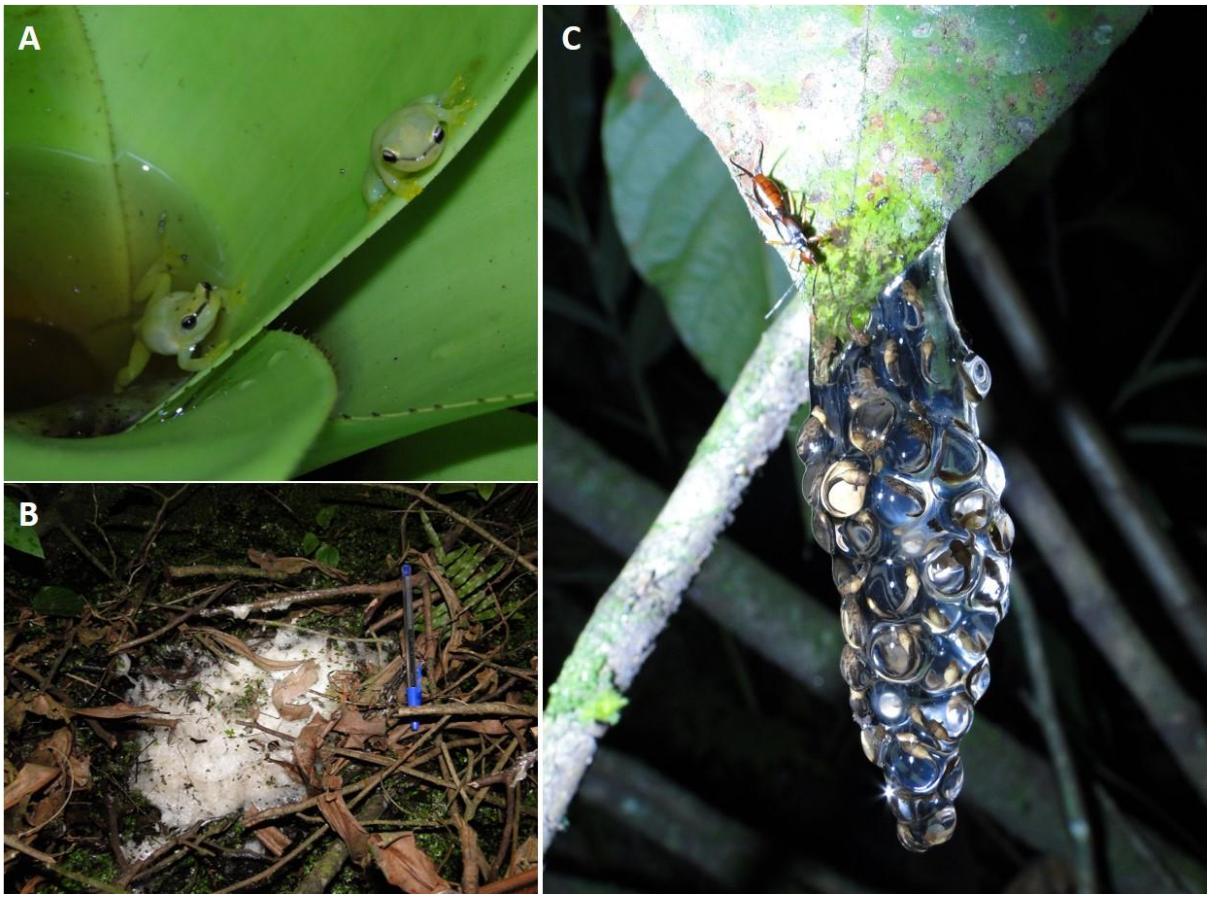

Figure 1. Examples of particular breeding sites used by anuran amphibians. A) Reproductive site of *Phyllodytes melanomystax* (Anura: Hylidae) inside a bromeliad. B) Foam nest of a species in the *Physalaemus signifer* group (Anura: Leptodactylidade) on the humid forest floor. C) Arboreal eggs deposited by *Dendropsophus berthalutzae* (Anura: Hylidae).

REVIEW OF CURRENT PREDICTORS USED IN AMPHIBIAN DISTRIBUTION MODELING

The search of amphibian distribution modeling articles

To characterize the current practices regarding variable selection, we performed a web search to extract original peer reviewed articles dealing with SDMs of amphibians. The target of the search was to record published articles (year 1997 to 2017) in ISI Web of Science (WoS) and the search was performed using the query ("species distribution model*" OR "habitat model*" OR "ecological niche model*" OR "niche model*" OR "habitat distribution model*" OR "habitat suitability model*" OR "niche-based model*" OR "bioclimatic envelope model*") AND (“amphibian*” OR “anuran*” OR “caudata*” OR “gymnophiona*”) following Guisan et al. (2013).

We surveyed 342 articles, from which we manually excluded 143 because they did not use correlative models or because they focused on modeling the potential distribution of the chytrid fungus (*Batrachochytrium dendrobatidis*), an amphibian pathogen considered as new driver of global amphibian decline (Penner et al., 2013). So, for the remaining 199 papers we recorded the methods used to select the predictor variables and the type of variables included in the models (Appendix 1). After the compilation, we divided the predictors into nine variable categories, partially following Mod et al. (2016): temperature, water, topography, land cover, biotic, hydrology, soils, solar radiation, and geology. Each of these main categories was then subdivided for a better description of the variables used in amphibian distribution models. The temperature and water categories (i.e., climatic variables) were divided into mean, extreme, and seasonality variables; water category had two additional sub-classes: water balance and air moisture. Topographic variables were divided into elevation, slope, aspect, and topographic index. Biotic variables were divided into normalized difference

vegetation index (NDVI), enhanced vegetation index (EVI), anthropic, canopy cover, leaf area index (LAI), fraction of absorbed photosynthetically active radiation (FAPAR), and net primary productivity (NPP). The sub-class anthropic included disturbances generated by human action (i.e., deforestation, fire, noise, and artificial light). Urban areas were included in the land cover category. The hydrology variables were divided into distance from rivers, flows direction, stream order, density of stream, and hydrography. The soils variables were divided into types of soils, texture, moisture, and pH. The land cover, solar radiation, and geology variables were not divided in classes.

Summary of predictor variables in articles

The temperature- and water-related variables were the most used, appearing respectively in 189 (94.9 %) and 187 (93.9 %) studies (Figure 2), being that 71 studies (35.6 %) used only bioclimatic variables of WorldClim database, derived from the monthly temperature and rainfall values (Hijmans et al. 2005). This same pattern of use of these variables was observed in recent revisions of methodologies and variables used in SDM (e.g., Mod et al. 2016, Fourcade et al. 2017). The WorldClim database is the most common source of climate data for SDM studies (Booth et al. 2014). This widely used database offers climatic data for 19 bioclimatic variables, covering the global land areas, except Antarctica, in four different spatial resolutions (Hijmans et al. 2005).

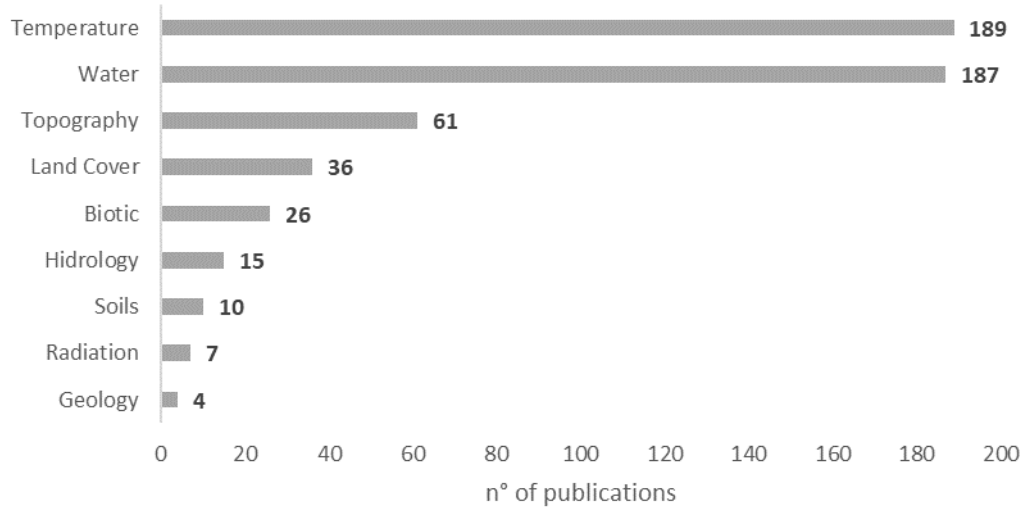

Figure 2. Category of the selected variables and the respective numbers of publications that used them. Temperature and water were the most used in amphibian distribution models.

Regarding the selection of variables, an important step of the SDM studies (Fourcade et al. 2017), only 106 (53.2 %) studies used some method of selection of predictors, of which 73 (36.6 %) selected variables based on some statistical criteria and 33 (16.5 %) used selection based on the biology/ecology of the species (Figure 3). Considering only the studies that made selection of variables (n = 106), 62 (58.4 %) also used only bioclimatic variables derived for WorldClim (e.g., Hijmans et al. 2005). This example of the use of WorldClim shows that although there are several methods of selection of variables, most of the studies are still using only a subset of climatic variables. In addition, the selection of variables from a limited set of climatic variables had the aim to exclude only the cross-correlated variables rather than inserting new predictors essential for the amphibians.

In general, there was a decrease in the use of variables related to temperature and water and an increase in the use of predictors included in the categories topography, land cover, biotic, and hydrology (Figure 3) when the selection of variables based on the biology/ecology of amphibians was used. As an example, some authors justified the use of

these non-climatic predictors emphasizing that they were important to characterize breeding sites (Bani et al. 2015), to delimit the natural areas (Ficetola et al. 2015), and to predict the occurrence of the species in urban areas (Milanovich et al. 2012).

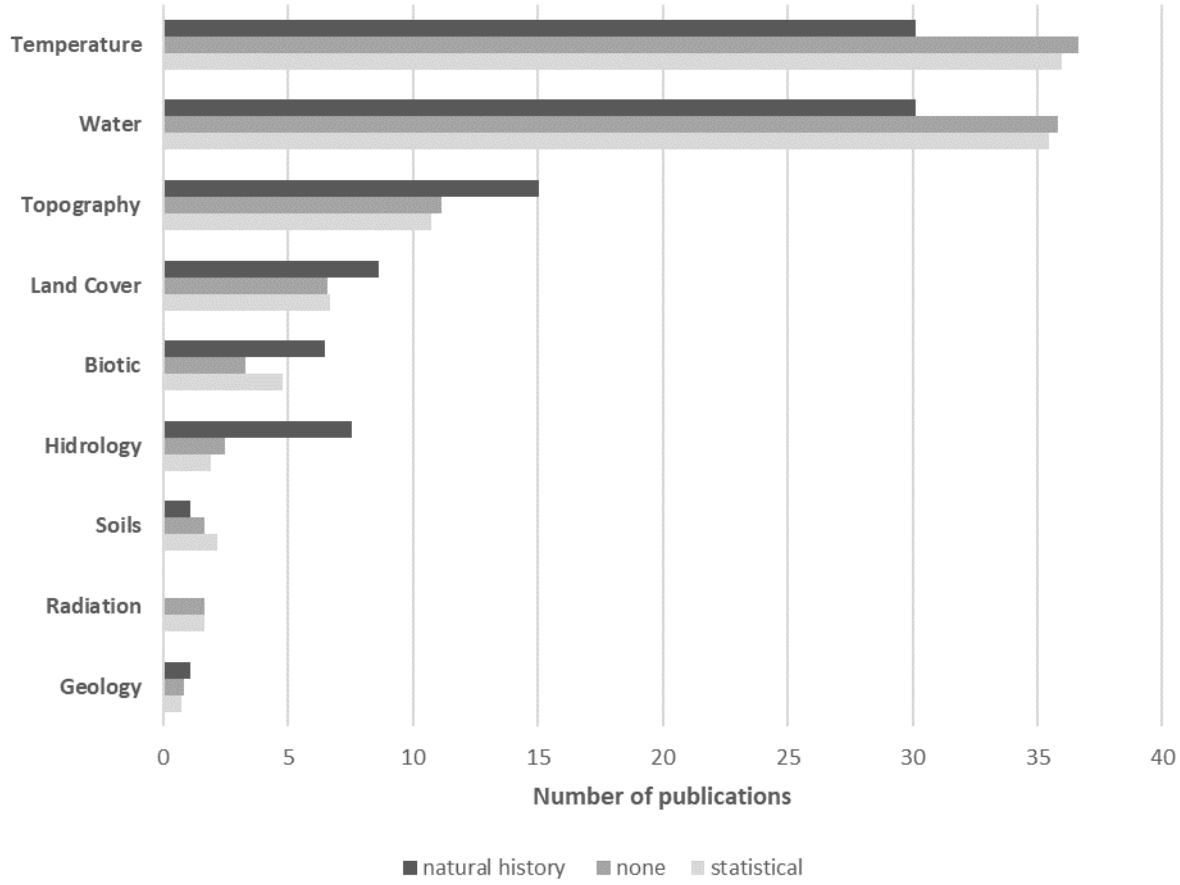

Figure 3. Use of predictors considering the selection of variables based or not on the natural history of amphibians and statistical criteria.

Furthermore, by analyzing the temporal use of the predictor variables, it was possible to observe an intensification of the use of non-climatic variables since 2009 (Figure 4). This is due to the greater availability of variables derived from remote sensors launched in the decade of 2000, mainly the products derived from the Moderate Resolution Imaging Spectroradiometer (MODIS) (e.g., vegetation index, land surface temperature and emissivity, and land cover) and Shuttle Radar Topography Mission (SRTM) (e.g., elevation).

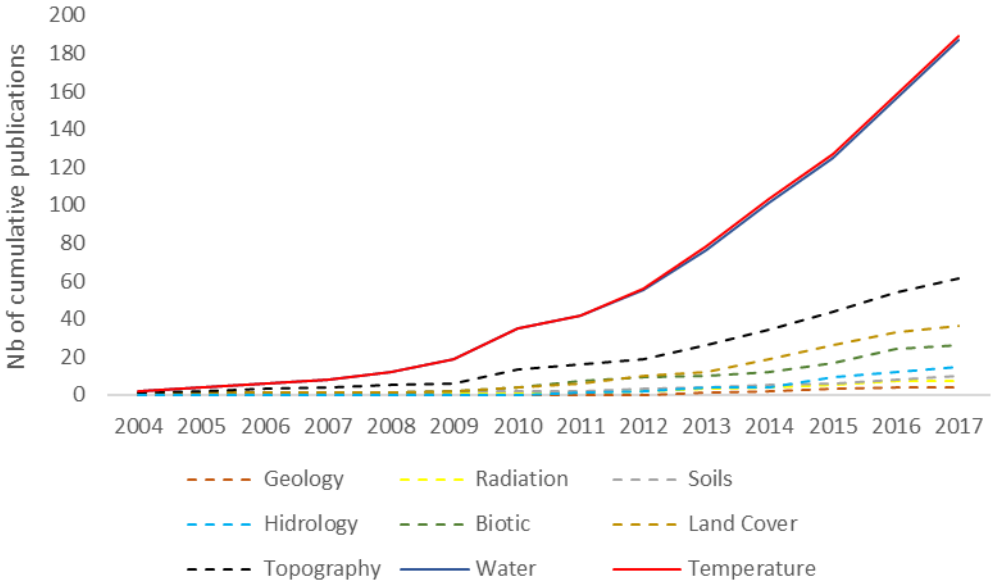

Figure 4. Temporal use of the predictor variables showing an increase of the use of non-climatic variables since 2009.

Description of the variables used in amphibian distribution models

Temperature and water

As mentioned above, temperature- and water-related variables were the most used in amphibian distribution models (189, 94.9 % and 187, 93.9 %, respectively). In our study, we divided the temperature category into three classes. The first, the extreme temperature was the most used in the studies (167, 83.91 %), followed by mean temperature (161, 80.90 %) and seasonality of temperature (155, 77.88 %). The water category was divided into five classes. The first, the extreme precipitation was the most used in the studies (156, 78.39 %), followed by mean precipitation (152, 76.38 %), seasonality of precipitation (145, 72.36 %), air moisture (8, 4.02 %), and water balance (6, 3.01 %). However, only 28 studies (28, 14.07 %) used exclusively extreme or seasonal variables.

Considering temperature variables, extreme and seasonal variables, rather than means, seems to impact more significantly on the ecology of amphibians, representing the tolerance limits of geographic distribution (Duellmann 1999) and favorable conditions for reproduction of terrestrial amphibians (Hillman et al. 2009). For example, Wiens et al. (2006) showed the importance of seasonal temperature in limiting the geographic distribution of hylids in temperate areas. In this work, analyses of the northern range limits of four tropical treefrog clades in northeastern Mexico suggest that these clades fail to extend their ranges further north into temperate regions because they are unable to tolerate the cooler winters (i.e. higher temperature seasonality) in north of their current ranges. Further, SDM using temperature seasonality alone accurately predicts the northern range limits of these clades (e.g., Wiens et al. 2006).

In this sense, we encourage the use of temperature- and water-related variables that express seasonality (e.g., annual range in temperature and precipitation) and extreme or limiting environmental factors (e.g., temperatures of the coldest and warmest months, and precipitations of the wet and dry quarters). Currently, there is a range of variables available in different resolutions, for example, WorldClim (Hijmans et al. 2005), Worldclim 2 (Fick & Hijmans 2017), Chelsa Climate (Karger et al. 2017), and MerraClim (Vega et al. 2017).

Considering water variables, in addition to precipitation-related variables, the inclusion of variables related to air moisture and water balance can increase the accuracy of the amphibian distribution models, mainly for those species that depend of the availability of free water in the form of moisture on rocks and leaf litter.

Another important issue identified regarding the use of temperature- and water-related variables is on the resolution and accuracy of these data sets. Temperature and water measurements are typically obtained by interpolating sparse measurements and neglecting the

impact of local topography, land cover, or waterbodies on local temperatures (Mod et al. 2016). In this sense, the use of remote sense climate data, generated without interpolation and geographical biases, can increase accuracy of the models (He et al. 2015).

We found that only three (1.50 %) studies used temperature variables derived from remote sensing. We encourage the use of this type of data, especially in fine scale studies (i.e., conservation planning). Currently, there are products derived from remote sensors that can be easily used in SDM. For example, MODIS Land Surface Temperature data is increasingly being used in SDMs (He et al. 2015). For precipitation, the Climate Hazards Group InfraRed Precipitation with Station data (CHIRPS) incorporates 0.05° resolution satellite imagery with in-situ station data to create gridded rainfall time series for trend analysis and seasonal drought monitoring (Funk et al. 2015). Recently, bioclimatic layers were generated from these data (MODIS/CHIRPS) (Deblauwe et al. 2016). Another option for using data derived from remote sensors is Worldclim version 2. Although using interpolated data, weather station data were interpolated with covariates including elevation, distance to the coast, and three satellite-derived covariates: maximum and minimum land surface temperature as well as cloud cover, obtained with the MODIS satellite platform (Fick & Hijmans 2017).

Topography

Unlike variables related to temperature and water, the variables related to the topography are not directly essentials to physiological ecology of amphibians, but their effect is to generate change in temperature, humidity, and availability of breeding sites (e.g., Siqueira & Rocha 2013). Topography is an important control on hydrological processes (Hjerdt et al. 2004). The availability of water in streams, puddles, and bromeliads can vary with altitude. Locations at high altitudes potentially receive higher levels of ultraviolet (UV)

radiation. Eggs and tadpoles can suffer high mortality/deformation due to exposure to UV radiation in mountain areas (Broomhall et al. 2000)

Topography-related variables were the third most used variables (61 studies, 30.65 %). We divided the topography category into four classes. The first, the elevation was the most used in the studies (48, 24.12 %), followed by slope (28, 14.07 %), aspect (17, 8.54 %), and topographic index (12, 6.03 %). We attribute to two factors the great use of variable elevation. The first is that this variable represents the most explicit measure representing an altitudinal variation. The second is the large availability of elevation variables derived from digital elevation models (DEM). Since the 2000s, some international initiatives made effort to obtain a complete high-resolution digital topographic database of Earth (e.g., Shuttle Radar Topography Mission – SRTM and Advanced Spaceborne Thermal Emission and Reflection Radiometer – ASTER). Currently, several databases make this data available in several spatial resolutions. For example, EarthEnv-DEM90 digital elevation model was derived from SRTM and ASTER data products (Robinson et al. 2014) and is available in the EarthEnv website (http://www.earthenv.org/).

However, although elevation is the main variable currently used, other variables derived from topography have the potential to increase the accuracy of the models. One of the main variables that could be considered in the context of topography is slope. Depending on the degree of slope, it can model the distribution of amphibians by modifying characteristics of water bodies (i.e., flowing or standing water). High slopes (i.e., escarpments and peaks) provide the formation of first order rivers, usually with low water volume but with high water flow. In this sense, for aquatic amphibian species and for the species that lay eggs in running water, the insertion of these variables can add essential information to the model. For example, these mountain streams are specific habitats for species of anurans of the

Neotropical family Hylodidae (*Crossodactylus, Hylodes, Megaelosia*; 47 species) (Haddad et al. 2013, Frost 2018) and salamanders of the family Cryptobranchidae (Aardema et al. 2018).

The topographic indexes were the less widely used topography-related variables. The application of topographic index is very common in geomorphological and hydrological studies. Topographic index maps are grids derived from digital elevation models (DEMs) and are constructed to highlight physiographic features of interest. One of the most used indexes is the topographic wetness index (TWI), which combines local upslope contributing area and slope, being commonly used to quantify topographic control on hydrological processes (Sørensen et al. 2006). Currently, this index has been used as a solution to find the distribution of flash-flood-prone areas (Pourali et al. 2016). For amphibians, the TWI would be a relevant predictor variable to identify wetter areas that could serve as breeding sites for species that have both direct and indirect development, especially those reproducing in lentic water. Many species of anurans from the family Hylidae (genera *Dendropsophus*, *Boana*, and *Ololygon*) and Leptodactylidae (genera *Leptodactylus* and *Physalaemus*) reproduce in temporary puddles formed after heavy rains. Depending on the spatial resolution used, the TWI has the potential to indicate the most suitable areas for the formation of these pools.

Land cover

Land cover-related variables were the fourth most used variables (36 studies, 18.09 %). In the past, land cover was used only in the categorical variable format. Categorical variables take only a limited number of discrete values such as vegetation type (on a discrete scale) (Phillips & Dudík 2008). For example, the MaxEnt program for modeling species distributions accepts the inclusion of categorical data (Phillips et al. 2006). Some studies have used categorical vegetation data to cut out the predicted areas of the model that were not

known as habitats for the species (e.g., urban areas and deforested places) (Loiselle et al. 2010, Paviolo et al. 2016).

However, land-cover data are provided with a discrete class assigned to each pixel, ignoring within-pixel heterogeneity (Blanco et al. 2013). Currently, there are products in continuous format, based in remote sensing. These continuous variables take arbitrary real values which correspond to measured quantities such as altitude, annual precipitation, and maximum temperature (Phillips & Dudík 2008). Land-cover data have been incorporated into SDM to improve model accuracy (Tuanmu & Jetz 2014). We compiled 36 studies that used land use as a predictor variable and of these only four studies used mappings derived from remote sensors. For instance, Sillero et al. (2012) tested the efficiency of using remotely sensed imagery in the SDMs of Iberian Herps. Results showed that satellite imagery can produce accurate SDM, independently of the modeling technique or the dataset used.

An example of land-cover in continuous format is the Global 1-km Consensus Land Cover database available in the EarthEnv project (http://www.earthenv.org). This dataset integrates multiple global remote sensing-derived land-cover products and provide consensus information on the prevalence of 12 land-cover classes at 1-km resolution (Tuanmu & Jetz 2014). This database has relevant variables to be inserted in amphibian distribution models, mainly for those habitat specialist species. For example, the class evergreen broadleaf trees can be used to increase the accuracy of models of forest specialist species. On the other hand, the classes cultivated and managed vegetation and barren can be used to model species of open area generalist amphibians that tolerate anthropic disturbance.

Biotic

Biotic-related variables were used by 26 studies (13.06 %). The human influence variable was the most used in the studies (11 studies, 5.52 %), followed by NDVI (9, 4.52 %),

EVI and canopy cover (5, 2.51 %), LAI (2, 1.00 %), FAPAR, and NPP (1, 0.50 %). Except for human influence, all other variables are related with vegetation characteristics. Vegetation can be an important predictor of species' habitat, acting as a proxy for sources of food availability or shelter (He et al. 2015). Although several amphibians are herbivores in the larval stage, in the post-metamorphic life they are carnivores, feeding mainly on invertebrates (an exception is the anuran *Xenohyla truncata* whose metamorphosed individuals eat fruits besides invertebrates; Silva & Britto-Pereira 2006). So, for amphibians, vegetation will not be a relevant proxy for food availability but may be an important proxy of habitat. In addition, many of the amphibian predated invertebrates are herbivores. So indirectly there may be a strong relationship between vegetation and food available to amphibians.

Our review showed the use of variables derived from remote sensors that indicate vegetation productivity (NDVI and EVI), plant canopy (LAI and Canopy Cover), and photosynthetic activity (FAPAR and NPP). An example of this was the study by Sangermano et al. (2015) that used NDVI, acquired between 2000 and 2011, to verify the habitat degradation for four species of amphibians in the Dominican Republic. In another study, Bisrat et al. (2011) used four MODIS biomass/greenness products (LAI, NDVI, FAPAR, and EVI) to predict the potential of invasion of *Eleutherodactylus coqui* in Hawaii.

In this sense, we encourage the use of biotic derived variables for modeling species in which habitat specificity is a striking feature. For example, vegetation indices (NDVI, LAI, EVI, FAPAR, and NPP) may be good predictors of strictly forest species, especially for those living in primary forests and dependent on forest canopy shading (e.g., Heinen 1992, Raxworthy & Nussbaum 1994, Gardner et al. 2007).

Hydrology

Some amphibians have strong dependence on aquatic environments, especially those species with adults having a strictly aquatic habit, as well as those that depend on water for egg deposition and tadpole development. However, despite the importance, the hydrology-related variables are few used in amphibian distribution modeling (15 studies, 7.53 %). The distance from rivers and hydrography variables were the most used in the studies (7, 3.51 %), followed by flow direction (5, 2.51 %), stream order, and density of stream (1, 0.50 %). The distance from the rivers is a relevant variable for amphibians that lay their eggs in lotic environments (Becker et al. 2007). Although these species can live independently of the body of water, seasonally these species migrate to the proximity of the body of water in the reproductive period (Duellman & Trueb 1994). In addition, this proximity to the rivers keeps the soils moister, favoring also species of direct development.

For strictly aquatic amphibians, flow direction, stream order, and density of stream characterize the different physical characteristics of water bodies. Currently, the EarthEnv project provides a dataset of freshwater-specific environmental variables that can be used in amphibian distribution models (Domisch et al. 2015). In this sense, we encourage the use of this dataset in amphibian distribution models. This dataset contains a variety of different metrics of the upstream environment along the stream network (climate, topography, land cover, surface geology, and soil), resulting in a total of 324 layers. The monthly climate variables were summarized into 19 long-term climatic variables following the "Bioclim" framework (e.g., Domisch et al. 2015).

Soils and geology

Soils- and geology-related variables were used by 10 (5.02 %) and 4 studies (2.01 %), respectively. The most commonly used soil-related variable was type of soil (6 studies, 3.01

%), followed by pH (3 studies, 1.50 %), texture (2 studies, 1.00 %), and moisture (1 study, 0.50 %). Soil-related variables may be relevant for modeling terrestrial species, especially those that deposit their eggs directly in the soil or bury themselves and hibernate. Variables such as pH and soil moisture can directly influence the availability of reproductive sites. An example of this is the Neotropical Brachycephalidae family in which most known species deposit terrestrial eggs (Haddad et al. 2013). On the other hand, soil type and texture may be relevant information for fossorial and semifossorial species, especially for species in the Order Gymnophiona. The insertion of these variables may increase the predictive map quality for this group, which is one of the least studied of amphibians.

Geology variables were not divided in sub-classes, since in our review we found studies that used only surface geology as a variable. The surface geology can be described as the rock formations, structures, and other features as seen at the Earth's surface (Morris 2000). Some terrestrial amphibians can live in rocky environments with sparse vegetation, typical of high-altitude environments. As examples of species that tolerate these habitats, and for which ecology and natural history have already been studied, we can cite the anuran *Oreophrynella quelchii* that occurs in the summit of Mount Roraima in Venezuela, Guyana, and Brazil, and from Wei-Assipo-Tepui in Guyana (Kok et al. 2018); and the species of salamander *Triturus carnifex* which occurs in regions of high altitudes in Europe (Arntzen & Thorpe 1999). In this sense, information on surface geology can add important information in the geographic distribution models of these species, mainly of the species that occur in high altitudes. Currently, some databases provide information about soil and geology. The database SoilGrids (https://soilgrids.org) have a collection of updatable soil property and class maps of the world at 1 km / 250 m spatial resolution produced using automated soil mapping based on machine learning algorithms (Hengl et al. 2017). In addition, with the recent launch of

NASA's Soil Moisture Active Passive (SMAP) Mission, high-resolution soil moisture data (3 and 9 km) with global coverage will also soon be available (He et al. 2015).

Solar radiation

Only seven studies used variables related to solar radiation. None of these studies justified the use of this predictor variable and its influence in the modeling context. In amphibians solar basking far from water sources is relatively uncommon since the highly permeable amphibian skin does not represent a significant barrier to the accompanying risk of losing water by evaporation (Tattersall et al. 2006). Experiments have shown that ultraviolet radiation can increase frequencies of mortality and malformation in several amphibian species (Blaustein et al. 1997). These studies suggest that UV radiation (especially UV-B) can damage the cellular DNA of amphibian embryos and larvae (Oromi et al. 2007).

However, the basking behavior of *Bokermannohyla alvarengai* shows that amphibians can develop interesting strategies to cope with high solar radiation. Due to the low temperatures, this species spends a significant amount of the day exposed to full sun and relatively high temperatures (e.g., Tattersall et al. 2006, Centeno et al. 2015). *Bokermannohyla alvarengai* is a species restricted to areas above 1,000 meters of altitude in the Espinhaço mountain range, in the states of Minas Gerais and Bahia, Brazil (Eterovick & Sazima 2004).

In this sense, solar radiation-related variables may limit and, in some cases, favor the distribution of some species of amphibians. Its use in amphibian distribution models may be important mainly for amphibian inhabiting open area and/or xeric environments, as well as for fossorial or forest species that live under the forest canopy. Currently, the WorldClim version 2 dataset provides solar radiation variable (kJ m-2 day-1) in fine resolution.

CASE STUDIES

Case study 1: Selection of climate data sets for modeling the potential distribution of a widespread amphibian

In this case study we tested the performance of the models using a set of bioclimatic variables derived from interpolations between sparse station data, global circulation models, and new set of satellite-based climatic predictor data. As response variable, we used the occurrence of a widespread Neotropical amphibian *Leptodactylus chaquensis* Cei, 1950. This species is in the *Leptodactylus latrans* species group (de Sá et al. 2014) and has a wide range distribution occurring in different biomes (see details below), including the Amazon where there is a climate data gap (Hijmans et al. 2005).

Our hypothesis is that a new set of climatic data obtained from remote sensors and global circulation models has potential to improve modelled species. We believe that these climatic data sets are useful for modeling regions where there are data gaps, such as the Amazon biome. In this region there are few climate stations, so the real resolution of the data is probably much poorer than nominal pixel size (Zuquim et al. 2014). In contrast, the remotely sensed climate data are continuously observed without interpolation and geographical biases (He et al. 2015).

Methods

We used occurrence localities of *Leptodactylus chaquensis* collected in the field by GPS device or that contained accurate collection information that allowed us to get the coordinates using Google Earth. In total, 819 points of occurrence were used from specimens housed in collections from Argentina, Brazil, Paraguay and Uruguy (CHUNAM, LGE, MFA-ZV-H, CFBH, CHUNB, UFRN, UFBA, UFMG, ZUFG, IIBP, ZVCB; collection abbreviations follow Sabaj 2016). All the registered specimens had their taxonomy checked

based on vouchered specimens and through DNA sequencing, which indicated that all populations belong to a single species. Records previously assigned to *L. macrosternum* (currently only known from type series and locality; de Sá et al. 2014) from Cerrado, Caatinga and Amazon regions were compared and re-identified as *L. chaquensis* based on molecular, morphological and bioacustic data (data not shown; detail on molecular diversity and population structure patterns will be discussed elsewhere).

We used three criteria to select occurrence points: (i) points located within the same pixel (with aproximately 10 km² cell size – resolution) were considered as a single occurrence, (ii) points located in county centroids were excluded, and (iii) occurrence points collected before the year 1970 were also excluded. In total, 819 points of occurrence were used.

As predictor variables, a set of bioclimatic variables derived from five climatic data sets was used: WorldClim version 1 (1960-1990) (Hijmans et al. 2005), Worldclim version 2 (1970-2000) (Fick & Hijmans 2017), CHELSA (Climatologies at High Resolution for the Earth's Land Surface Areas) (1979-2013) (Karger et al. 2017), MERRAclim (Vega et al. 2017), and NASA Moderate Resolution Imaging Spectroradiometer Land Surface Temperature (MODIS) sensor MOD11C3 (2001-2013) and Climate Hazards Group InfraRed Precipitation with Stations (CHIRPS) (1981-2013) precipitation dataset (Deblauwe et al. 2016). All predictor variables have 5 minutes of spatial resolution and we run the models in whole South America extent.

The data set of WorldClim version 1 and version 2 was built using the method of splines interpolation between weather stations (Hijmans et al. 2005, Fick & Hijmans 2017). However, the Worldclim version 2 was built using interpolated data and three satellite-derived

covariates: maximum and minimum land surface temperature as well as cloud cover, obtained with the MODIS satellite platform (Fick & Hijmans 2017).

The CHELSA is based on a quasi-mechanistic statistical downscaling of the ERA-interim global circulation model with a GPCC bias correction. The temperature algorithm is based on statistical downscaling of atmospheric temperatures. The precipitation algorithm incorporates orographic predictors including wind fields, valley exposition, and boundary layer height, with a subsequent bias correction (Karger et al. 2017). Finally, the data set of MERRAclim and MODIS/CHIRPS are satellite-based climatic predictor data (Deblauwe et al. 2016, Fick & Hijmans 2017, Vega et al. 2017).

We modeled using four bioclimatic variables: annual mean temperature (BIO 1), temperature seasonality (standard deviation x 100) (BIO 4), annual precipitation (BIO 11), and precipitation seasonality (coefficient of variation) (BIO 15). These non-correlated variables are available in all climatic models used and express the average values and seasonality found in the region of occurrence of the species, allowing comparison between climatic data sets.

We used four commonly used algorithms to predict the amphibian distribution models: Bioclim (Nix 1986, Busby 1991), Gower (Carpenter et al. 1993), MaxEnt (Phillips et al. 2006), and SVM (Vapnik 1995, Drake & Bossenbroek 2009). All algorithms were implemented in the dismo package in R (available at https://CRAN.R-project.org/package=dismo). For each algorithm we ran 10 replicates with 75 % of occurrence for training model and 25 % for model test. We evaluated the models by the area under the receiver operating characteristic curve (AUC) value, a threshold-independent measure of overall model performance (mean ± standard deviation) (Fielding & Bell 1997, Manel et al.

2001). The AUC is a measure of the area under the ROC ranging from 0.5 (random accuracy) to a maximum value of 1.0 (perfect discrimination).

We estimated “maximum sum of specificity and sensitivity” threshold values for each generated model and then binarized the continuous suitability maps (presence or absence). This threshold value is recommended when using presence only algorithms (Liu et al., 2016, Moraes et al., 2019). After this, we used ensemble forecasting approach (Araújo & New 2007) to obtain a consensus map for each climate dataset. Following Diniz-Filho et al. (2009), to assess individual model variability sources, we separated and mapped uncertainties in forecast ensembles. For this, we performed a two-way ANOVA for each grid cell using suitability as response variable and the methodological components (climatic data sets and algorithms) as explanatory variables.

Results and discussion

The figure 5 shows the ensemble models for five climatic data sets used. In general, CHELSA, MERRAclim, and Worldclim version 1 had higher AUC test values. However, there was no significant difference between the mean AUC test values of the models (Figure 6). This result encourages the use of these new climatic data sets, since they obtained performance similar to Wordclim version 1, a climatic dataset widely established in the SDM studies (Fick & Hijmans 2017).

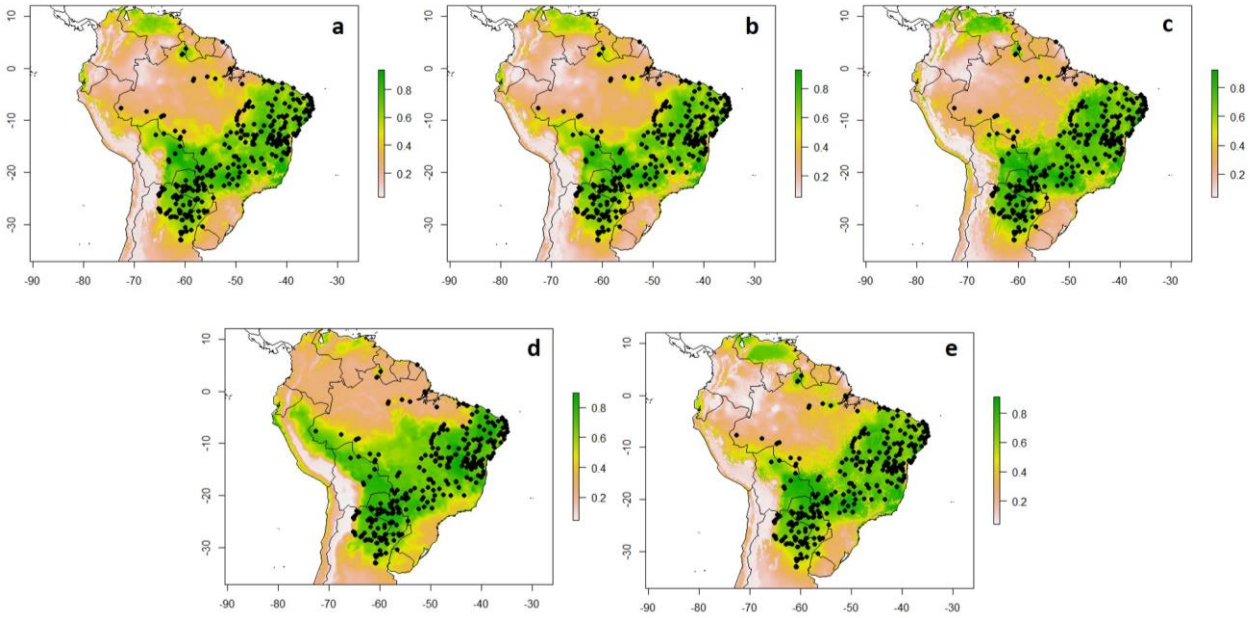

Figure 5. Ensemble models from the five climatic models used: (a) WorldClim version 1 (Hijmans et al. 2005), (b) Worldclim version 2 (Fick & Hijmans 2017), (c) MOD11C3 land surface temperature (MODIS sensor, 2001-2013) and CHIRPS (1981-2013) precipitation dataset (Deblauwe et al. 2016), (d) MERRAclim (Vega et al. 2017), and (e) CHELSA (Karger et al. 2017).

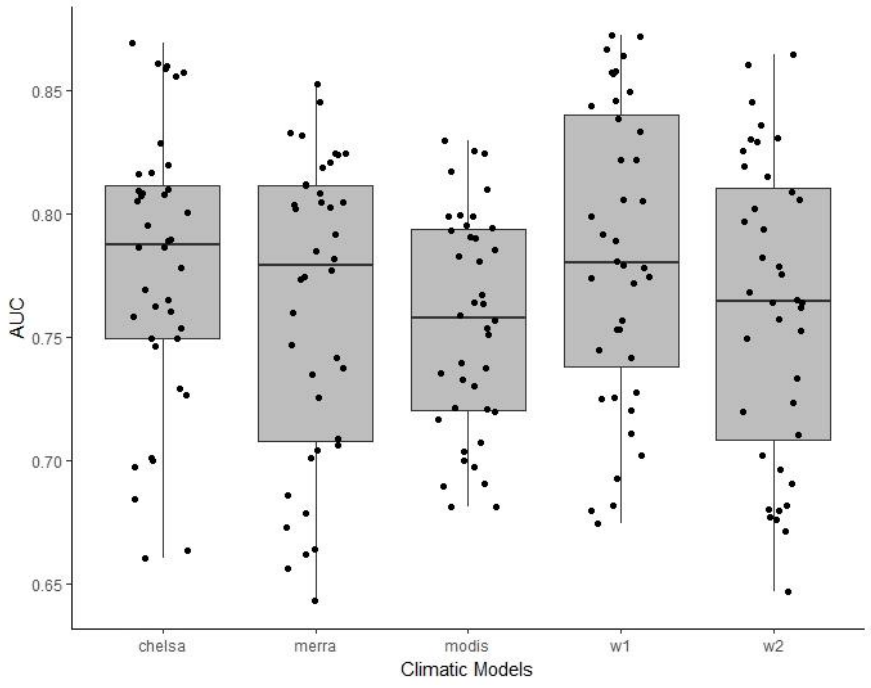

Figure 6. Box plot graph of test AUC values for each climatic data set used in the study.

Although the two-way ANOVA applied to each cell indicated that climatic data sets explained a low proportion of the total sum of squares with a median value of 10 %, the interaction between climatic data sets and the algorithms explained a high proportion of the total sum of squares with a median value of 65 %, ranging from 0 up to 99 % (Table 1). The highest values for this interaction were found in practically the whole South America extension used to run the models, except for some areas located on Andes ridges, far west of Amazonia, and in the central region of Brazil (Figure 7).

Table 1. Median proportions of the total sum of squares from the two-way anova performed for each grid cell, evaluating the relative contributions of algorithms and climatic data sets.

Source	SS (%)	
	Median	**Min-Max**
Algorithms	0.24	0-0.84
Climatic data sets	0.10	0-0.66
Algorithms x Climatic data sets	0.65	0-0.99

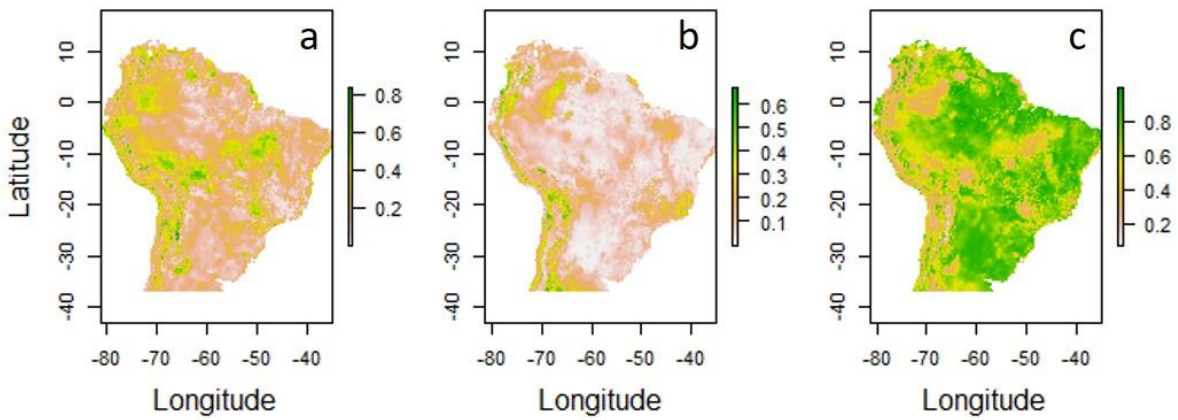

Figure 7. Proportion of the total sum of squares accounted for by algorithms (a), climatic models (b), and the interaction between these factors (c).

Regarding the predictive maps generated, after the ensemble application, it was possible to notice that MODIS/CHIRPS, MERRAclim, and CHELSA generated maps of realistic potential occurrence with the expected distribution of the species. Even without using a layer of land use, satellite data seem to differentiate climatically from forest and non-forest areas. Data from remote sensors possibly captured the temperature of the earth's surface in more detail, being a proxy also of the landcover since exposed soil areas may be climatically different from densely forested areas (e.g., He et al. 2015). Furthermore, the other climatic data sets (Worldclim versions 1 and 2) exhibited circular regions in the predictive maps that appear to be artifacts from the interpolation used to construct the climatic layer. These "circles" do not seem to represent a real phenomenon, which can disrupt the application of this map in projects that require greater spatial resolution, such as conservation planning projects (e.g., Guisan et al. 2013).

We understand that the performance of the algorithms and climate basis may change according to the species chosen. However, in this case study, the use of new set of climatic data sets provided a good performance to model geographic distributions of this species.

Case study 2: Selection of predictors based in traits of reproduction for improving the performance of amphibian distribution models

The central focus of this case study was to examine whether the predictors used in amphibian SDM studies correspond to the ecologically meaningful variables of amphibian species. Our hypothesis is that the selection of ecologically meaningful variables for each species can improve the performance of the models. For this, we selected a set of predictors and tested the effect of the inclusion of essential variables for four species of anurans [*Brachycephalus ephippium* (Spix, 1824), *Cycloramphus acangatan* Verdade and Rodrigues,

2003, *Dendropsophus jimi* (Napoli and Caramaschi, 1999), and *Hylodes caete* Malagoli, de Sá, Canedo, and Haddad, 2017] with distinct characteristics of natural history, mainly with significant differences in breeding and habitat occupation sites.

Methods

We compared three models for each species: the first used the only bioclimatic variables derived of WorldClim version 2 dataset (Fick & Hijmans 2017). The second model used the same bioclimatic variables derived of Worldclim version 2 dataset and the addition of remotely sensed variables selected for each species (Table 2). For the third model we used only selected variables of remote sensing. All predictors were resampling in 1 km^2 resolution (in Equator region). We calculated the correlations among WorldClim 2 and remote sensing variables to exclude the highly correlated ones ($r > 0.75$). With respect to bioclimatic variables, we selected eight relevant variables for all species, selecting only predictor variables that express seasonality and extreme temperatures and precipitations. For remote sensing variables we selected a set of non-correlated predictors for each species (Table 2).

Brachycephalus ephippium is a tiny frog that inhabits mountainous Atlantic coastal forest, from 750 m to 1200 m in elevation (Izecksohn & Carvalho-e-Silva 2001). In this sense, predictor variables related to topographic features are important for the modeling, so we selected slope and elevation as descriptive variables of the steep relief of this region (Table 1). In addition, *B. epphipium* deposits its eggs directly in the forest litter and it is reasonable to assume that occurrence of forests is an essential variable for this species. Thereby, we selected as predictor variables two types of forest cover of the Atlantic Forest biome (i.e., Evergreen Broadleaf Trees and Deciduous Broadleaf Trees) (Table 2).

Table 2. Climatic variables and data derived from remote sensing selected according to the ecology and natural history of target species of the case study.

	Variables	Source	Original spatial resolution	*Species*			
				Hylodes caete	*Cycloramphus acangatan*	*Brachycephalus ephippium*	*Dendropsophus jimi*
Climate	Isothermality (BIO3)	Worldclim v.2 (Fick & Hijmans 2017)	30 arc-second	X	X	X	X
	Maximum Temperature of Warmest Month (BIO5)			X	X	X	X
	Temperature Annual Range (BIO7)			X	X	X	X
	Precipitation of Wettest Month (BIO13)			X	X	X	X
	Precipitation of Driest Month (BIO14)			X	X	X	X
	Precipitation Seasonality (BIO15)			X	X	X	X
	Precipitation of Warmest Quarter (BIO18)			X	X	X	X
	Precipitation of Coldest Quarter (BIO19)			X	X	X	X
Remote Sensing	Elevation	Farr et al. 2007	90 m		X	X	
	Slope	Ambdata (Amaral et al. 2013)	90 m	X		X	
	Distance from Rivers	Rennó et al. 2008	30 arc-second				X
	Density of Rivers	Ambdata (Amaral et al. 2013)	30 arc-second	X	X		
	Topographic Wetness Index (TWI)	Present study (modified of Farr et al. 2007)	90 m	X			
	Evergreen Broadleaf Trees	Consensus Land Cover (Tuanmu & Jetz 2014)	30 arc-second	X	X	X	
	Deciduous Broadleaf Trees				X	X	
	Mixed/Other Trees						X

Hylodes caete is a recently described species in the family Hylodidae. The species of this family usually live near mountain streams and waterfalls, where they lay their eggs in the water (de Sá et al. 2015, Malagoli et al. 2017). This species occurs only in Serra do Mar Mountains, Southeastern Brazil. For *H. caete* we selected slope, distance from rivers, and density of rivers as variables describing the main characteristics of the water bodies used by this species. In addition, we chose a variable related to tropical forest (i.e., Evergreen Broadleaf Trees), since like *Brachycephalus ephippium*, this species usually occurs mainly in dense ombrophilous forests of the Atlantic Forest biome (Table 2).

Cycloramphus acangatan is found in Atlantic Forest remnants of Serra Mar in São Paulo state, Brazil. Individuals are usually found on the forest floor, not associated to water

bodies, but close to them. Breeding takes place by terrestrial larval development. This species seems to prefer pristine areas, but it is also present in forest fragments (Dixo & Verdade 2006). In this sense, for this species we selected elevation, distance from rivers, and two types of forest cover of the Atlantic Forest biome (i.e., Evergreen Broadleaf Trees and Deciduous Broadleaf Trees) as variables describing the main characteristics of the habitat used (Table 2).

Dendropsophus jimi is a generalist species that occurs only in the Cerrado biome in the states of São Paulo and Minas Gerais, Brazil. This species inhabits streams, marshes, and temporary ponds, where it also breeds. It also occurs in anthropogenic habitas (Caramaschi et al. 2004). For this species we selected topographic wetness index (TWI) and a type of vegetation cover that represents the open areas where the species occurs (i.e., Mixed/Other Trees) (Table 2).

The occurrence data were obtained in the catalogs of the following Brazilian collections: CFBH (Célio F.B. Haddad, Departamento de Zoologia, Universidade Estadual Paulista, Rio Claro, São Paulo, Brazil), MZUSP (Museu de Zoologia da Universidade de São Paulo, São Paulo), and MNRJ (Museu Nacional da Universidade Federal do Rio de Janeiro, Rio de Janeiro). We used only records that have geographic coordinates. These data were checked and filtered to avoid bias and errors, eliminating the occurrence points located in the centroid of municipalities and urban areas and collected before the year 1970. The points located within the same pixel (with aproximately 1 km² cell size – resolution) were considered as a single occurrence. The final data set included 19 occurrence points to *Cycloramphus acangatan*, 31 to *Hylodes caete*, 39 to *Brachycephalus Ephippium*, and 42 to *Dendropsophus jimi*.

We used four different algorithms to predict the amphibian distribution models: Bioclim (Nix 1986, Busby 1991), Gower (Carpenter et al. 1993), MaxEnt (Phillips et al.

2006), and SVM (Vapnik 1995, Drake & Bossenbroek 2009). For each algorithm we ran 10 replicates with 75 % of occurrence for training model and 25 % for model test, generating 40 models (10 replicates x 4 algorithms). The algorithms were modeled using "dismo" and "kernlab" R-packages (Hijmans et al. 2015, Karatzoglou et al. 2004).

We used ensemble forecasting (Araújo and New 2007) to determine a consensus map for each species. We estimated "maximum sum of specificity and sensitivity" threshold values for each generated model, and then binarized the continuous suitability maps (presence or absence). This threshold value is recommended when using presence only algorithms (Liu et al. 2016, Moraes et al. 2019). Also, we evaluated the models based on True Skill Statistic (TSS) values (Allouche et al. 2006). Prior to generating the suitability consensus map, all binarized maps were overlapped within the same algorithm and then between algorithms. The consensus maps (referred to as suitability map for each studied species) had suitability values varying from 0 to 40 and after divided by 40, indicating the frequency of models that predicted species presence in each cell. We also evaluated the models by the area under the receiver operating characteristic curve (AUC) value, a threshold-independent measure of overall model performance (Fielding and Bell 1997, Manel et al. 2001). To compare the extent of the predicted areas, we transformed each species map into binary maps, using the 10 percentile training presence. After this, we compare the distributional changes between models using SDMtoolbox 2.2b (Brown et al. 2017).

Results

In general, there were no significant differences between the AUC and TSS values for the models using only bioclimatic variables and the models using bioclimatic with remote sensor variables (Table 3). However, except for *Hylodes caete*, the use of only remote sensor variables generated low AUC values (Table 3).

Table 3. Mean AUC and TSS values for three models, for each species target in the case study. CLIM: Climate variables. RS: Remote sensor variables.

Species		CLIM	CLIM+RS	RS
Hylodes caete	AUC	0.95	0.94	0.97
	TSS	0.91	0.89	0.95
Cycloramphus acangatan	AUC	0.93	0.92	0.78
	TSS	0.87	0.84	0.60
Brachycephalus ephippium	AUC	0.87	0.87	0.78
	TSS	0.75	0.71	0.57
Dendropsophus jimi	AUC	0.82	0.81	0.65
	TSS	0.63	0.58	0.38

Regarding the size of the area, the models made with variables of climate and remote sensing obtained smaller areas (Figure 8). However, the models generated only with remotely sensed variables presented extensive areas when compared to the other models. This result shows the importance of using other model evaluation metrics. In the case of *Hylodes caete* the AUC value with the remote sensor variables were high (Table 3). However, the area predicted by the model using the same set of variables (only remote sensing) does not agree with the restricted geographic distribution of *H. caete*.

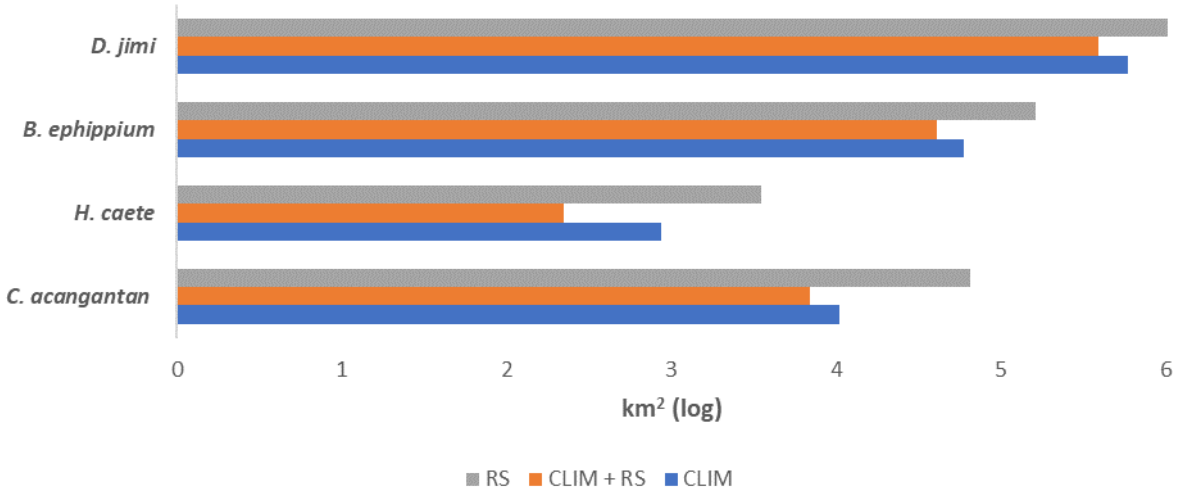

Figure 8. Size in km^2 of the area predicted for the three candidate models, for each target species in the case study. CLIM: Climate variables. RS: Remote sensing variables.

With respect to the distributional changes between models, comparing only the models made with climate and models made with climate and remotely sensed variables, the inclusion of the remote sensor variables caused a suitability contraction of the area for all species, adjusting the model in the areas in which the species may potentially occur. In *Brachycephalus ephippium* models, the inclusion of remotely sensed variables decreased the suitability in mountains in central São Paulo state and in regions with low altitude (i.e. Vale do Paraíba region), localities where the species does not occur. In the case of *Hylodes caete* models, the inclusion of remotely sensed variables decreased the suitability in more inland areas of Serra do Mar, composed by less rugged relief and, therefore, unsuitable for the presence of the species. Its expansion of suitability is observed to areas with rugged relief, located in crests and slopes of Serra do Mar. For *Cycloramphus acangatan* models, the inclusion of the remote sensor variables decreased the suitability in areas with low elevation, evidencing the preference of the species for areas above 750 m. In *Dendropsophus jimi* models, the inclusion of remotely sensed variables expands its suitability in open areas of

Mato Grosso do Sul state and contracted the northern and northeastern portions of the geographic distribution of the species (Figure 9).

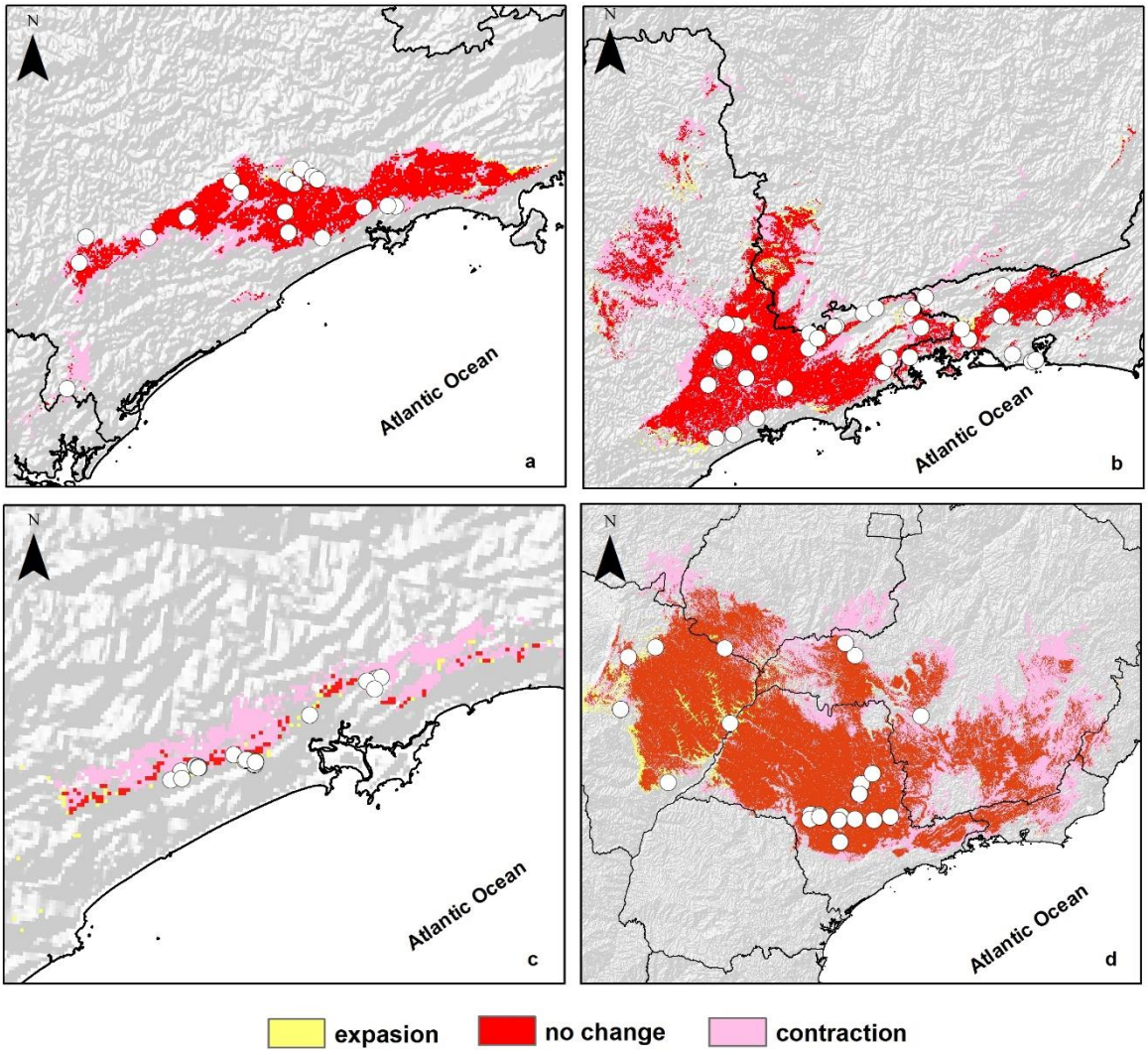

Figure 9. Distributional changes between models (a. *Cycloramphus acangatan*, b. *Brachycephalus ephippium*, c. *Hylodes caete*, and d. *Dendropsophus jimi*) comparing only the models made with climate and models made with climate and remote sensor variables. Note that the inclusion of the remote sensor variables caused the area contraction in suitability.

CONCLUSIONS

The main objective of this study was to review the current practices with the aim to improve the modeling process for amphibians, one of the most endangered vertebrate groups and of great importance for current conservation projects. Further refinement of the analyzes, especially including ecologically meaninful variables, can increase the quality of geographic distribution models, one of the essential tools in conservation planning.

The articles compiled here showed the generalized use of variables related to temperature and precipitation. The massive use of these variables is explained by the great importance that climate exerts on amphibians, as well as by the ease of use of these databases (e.g., Worldclim). However, although amphibians occupy a diverse range of environments, the compiled studies have shown a low use of landscape-related variables. In addition, a growing use of new predictor variables in amphibian distribution models is expected in the future, since new databases are being introduced, especially those derived from remote sensors launched in the decade of 2000.

Our case studies showed the effect of the use of important environmental variables on amphibians, but also considered the type of construction of this variable (i.e., interpolated or derived from remote sensor). Case study 1 showed that climate-derived remote sensor and global circulation models can be efficient to model regions where there are gaps in meteorological data sampling. In addition, the detailing of these environmental layers may be greater showing previously unreported temperature and precipitation differences in environmental layers made with climatic data obtained from conventional weather stations. The study case 2 showed that the inclusion of environmental variables that reflect important parameters of the ecology and natural history of the species can improve the quality of the geographic distribution models, also showing that the isolated use of landscape variables was

not efficient to leave the model more accurate. In general, the use of a set of climatic and landscape variables essential for each selected species resulted in more accurate models and is effective in restricting the models in regions more suitable for the species, and, in the case of *Dendropsophus jimi*, increasing the area of suitability in specific region (see again Figure 9).

We believe that this study can sensitize the researchers to this issue, informing that the modeling process is not straightforward to default procedures, but an important process based on the choice of variables and a certain understanding of the ecology and natural history of organisms.

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Appendix 1

The database containing the compiled and systematized articles that dealing with SDMs of amphibians is available here:

https://www.dropbox.com/s/f35ejm0hpor4nxx/giovanelli_etal_2019.xlsx?dl=0

Metadata:

ID: identification number
Selected: the article was selected (yes) or not selected (no) for the study
Year: year of publication
Title of article: title of publication
TEMPERATURE: the study used (1) not used (0) these variables - Mean Temperature, Extreme temperature, Seasonality of temperature. Source of data.
WATER: the study used (1) not used (0) these variables - mean precipitation, extreme, precipitation, seasonality of precipitation, air moisture, water balance. Source of data.
TOPOGRAPHY: the study used (1) not used (0) these variables – Elevation, Slope, Aspect, TRI, CTI, RI, TR, CAR, TWI, TOPOINDEX. Source of data.
HIDROLOGY: the study used (1) not used (0) these variables - Distance from rivers, Flows, order, density, hydrography. Source of data.
RADIATION: the study used (1) not used (0) these variables. Source of data.
BIOTIC: the study used (1) not used (0) these variables – NDVI, EVI, human influence, canopy cover, LAI, FAPAR, NPP. Source of data.
LANDCOVER: the study used (1) not used (0) these variables. Source of data.
SOILS: the study used (1) not used (0) these variables – type, texture, moisture, pH. Source of data.
GEOLOGY: the study used (1) not used (0) these variables. Source of data.
Type of selection of predictor variables.

Capítulo 2

Amphibian richness and conservation priorities identified by Stack Species Distribution Models - SSDMs: a case study of São Paulo state, Brazil

ORIGINAL ARTICLE

Amphibian richness and conservation priorities identified by Stack Species Distribution Models - SSDMs: a case study of São Paulo state, Brazil

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Abstract

In the last decade there was a great development in species distributions models (SDM). However, applications of these methods for decision making in conservation planning are scarce. The state of São Paulo has the largest accumulated knowledge of amphibians in Brazil, an important information to support the selection of priority areas for biodiversity conservation. In this context, the central focus of our study was to examine whether the existing geographical distribution data for the São Paulo state are efficient to identify high-value areas of amphibian richness and to detect gaps in the representation of species inside Protected Areas (PAs). First, we proposed an SDM-based methodology to model the geographic distributions of amphibians in fine scale using ecologically meaningful variables that correspond to the known ecological niche requirements of amphibian species. Further, we used the methodology of stacking species distribution models (S-SDMs) based on the predicted ranges of amphibian species by combining SDMs with three threshold criteria using presence-only data, and we compared the results in species richness and composition with ground-truth information. The maps showed that the cells with the highest species richness were concentrated, for all thresholds used, in the region of Serra do Mar. The final species richness map showed that species richness ranged from 0–4 species/km^2 in group A (species of genus *Brachycephalus*), 0–17 species/km^2 in group B (species that breeding in current water courses), 0–14 species/km^2 in group C (species that have direct development of eggs or terrestrial larval development), and 0–68 species/km^2 in group D (generalist species). The Friedman test showed that the S-SDMs were similar to the observed data, especially for the 20 % omission-percentage threshold, being an approach effective in capturing the patterns of species richness present in São Paulo state. These results may be useful to support environmental planning in this Brazilian state.

Keywords: Amphibians, conservation planning, species richness, species distribution models.

INTRODUCTION

The geographical distribution of species is a fundamental information for conservation planning. These spatially explicit data can facilitate the selection of priority areas for conservation, identify critical habitats, and predict biological invasions (Guisan et al. 2013). The last decade has experienced great advancement in Species Distributions Models (SDM) (e.g., Guisan & Thuiller 2005, Elith et al. 2006, Diniz-filho et al. 2009, Soberón & Nakamura 2009), and there are now numerous biological databases and free access tools that enable the creation of predictive geographic distribution maps (e.g., Hijmans et al. 2005, Munõz et al. 2011, Kass et al. 2018). However, despite the great progress with the theoretical basis necessary for ecological modeling (e.g., Elith et al. 2006, Elith et al. 2011, Merow et al. 2013), we still lack structured methods for decision making in conservation biology (Guisan et al. 2013).

Brazil contains 20 % of the world's biodiversity and has 335 federally protected areas covering approximately 760,000 km^2 (ICMBio 2018). Despite this environmental leadership, large infrastructure projects threaten significant portions of the remaining, unprotected ecosystems, putting endemic and endangered species at risk of extinction. Tools and methodologies based on species distribution models (SDMs) can help to predict such impacts to biodiversity. This is a big challenge, but new databases and remote sensing technologies, along with a recent public policy related to endangered species (MMA 2018), promise to generate knowledge for the creation of SDMs that support decision-making processes in this mega-biodiverse country.

In this context, the São Paulo state, located in the southeastern region of Brazil, stands out in the generation of knowledge aiming at the environmental conservation. In 2014, the government of the state of São Paulo, made available to the public the DataGEO Project

(http://datageo.ambiente.sp.gov.br/), whose aim is to structure, organize, and provide environmental and territorial information for the state of São Paulo through the construction of an infrastructure of spatial environmental data. With respect to the biological database, after the creation of the Biota-FAPESP Program, which supported biodiversity prospecting projects and the systematization of this information in a full access database (http://sinbiota.biota.org.br/), the knowledge of Brazilian biodiversity was greatly enhanced.

Amphibians, for example, experienced an increase of about 35 % in the number of species recorded for the state since 1998 because of the Biota-FAPESP Program. The number of recorded amphibian species in the state of São Paulo is 27 % of the total species richness of Brazil, which also reflects the fact that this state is the Brazilian region where amphibians have been studied the most (Rossa-Feres et al. 2011). Amphibians include excellent model organisms for biogeographic studies. They are ecologically specialized, with low dispersion capacity, and sensitive to environmental changes (Duellman & Trueb 1994), which make predictive modeling of their geographical distribution interesting (Giovanelli et al. 2010). Furthermore, the amphibians are the most threatened vertebrate group on the planet, with land use change being one of the main threats to amphibians (Becker et al. 2007).

In this context, the central focus of our study was to examine whether the existing geographical distribution data for the São Paulo state are efficient to identify high-value areas of amphibian richness and to detect gaps in the representation of species inside Protected Areas (PAs). First, we proposed an SDM-based methodology to model the geographic distributions of amphibians in fine scale using essential predictor variables that correspond to the known ecological niche requirements of amphibian species. The reproductive mode is a central aspect of amphibian life history that refers to specificities in the oviposition and tadpole developmental sites, among other traits (Haddad & Prado 2005). In this sense, including ecologically meaningfull variables that influence the reproductive contexts of

amphibians (e.g., streams, swamps, soil moisture, and vegetation) can increase the efficiency of distribution models, one of the essential tools in conservation planning (Guisan et al. 2013).

Further, we used the methodology of stacking species distribution models (S-SDMs) (Calabrese et al. 2014) based on the predicted ranges of amphibian species by combining SDMs with tree most used threshold criteria using presence-only data, and we compared the results in species richness and composition with ground-truth information provided by Vancine et al. (2018). Finally, we intend to evaluate the representation of richness of amphibians in PAs of São Paulo state.

METHODS

Study Area

The state of São Paulo has a total area of 248,808.8 km^2, divided into 645 municipalities and with a population of 44,749,700 inhabitants (DATAPEDIA 2018). The greatest human occupation occurs on the coast and in the metropolitan region of São Paulo city. In the interior, there are remnants of vegetation and great agricultural productivity, mainly sugar cane and livestock. Currently, the state's natural vegetation cover is 3,457,301 ha, corresponding to 13.94 % of its surface. The main phytophysiognomies are Atlantic Forest (that comprise the Restinga, Dense Ombrophylous Forest, Mixed Ombrophylous Forest, and Semideciduous Seasonal Forest) and Savanna (DATAGEO 2018). In general, the remaining natural vegetation is highly fragmented, with the exception of Serra do Mar, a large mountain range in the coastal.

The state of São Paulo shows five distinct climate types: 1) superhumid tropical climate in the coastal slope and cliffs of the Serra do Mar; 2) tropical altitude in the Atlantic Plateau region; 3) tropical hot and humid in the northwest region of the state; 4) subtropical in

the southern region; and 5) subtropical with dry winter and hot / humid summer on the Western Plateau (Nalon et al. 2008).

The state relief comprises an altimetric gradient ranging from 0 m above sea level on the coast to 2,797 m in the Serra da Mantiqueira. However, the territory of São Paulo is dominated almost entirely by the Plateau, being thus distributed: 7 % of surface above 900 m, 85 % of the surface between 300 and 900 m, and 8 % of the surface below 300 m (Nalon et al. 2008).

The Protected Areas (PA) of São Paulo state currently comprise 40,382.1 km^2. There are 142 PAs that cover 16 % of the territory of São Paulo state, being the largest area in the Serra do Mar region, one of the main remnants of Atlantic forest in Brazil. These include 74 PAs corresponding to the IUCN categories I-II (Strict Nature Reserve and Parks), 12 PAs corresponding to the IUCN categories III-IV (Natural Monument and Habitat/Species Management Area), and 56 PAs matching the IUCN categories V-VI (Protected Landscape/ Seascape and Protected area with sustainable use of natural resources) (Dudley 2008).

Species data

The occurrence points of amphibians were obtained in the catalog of the following Brazilian collections: CFBH (Departamento de Zoologia, Universidade Estadual Paulista, Rio Claro, São Paulo, Brazil), MZUSP (Museu de Zoologia da Universidade de São Paulo, São Paulo), and MNRJ (Museu Nacional da Universidade Federal do Rio de Janeiro, Rio de Janeiro). Only the records that had their geographical coordinates with accuracy in the scale of localities were used. These data were checked and filtered to avoid bias and errors, eliminating the occurrence points located in the centroid of municipalities and urban areas and collected before the year 1970. The points located within the same pixel (with aproximately 1 km^2 cell size – resolution) were considered as a single occurrence. The points of occurrence

without the geographical coordinates, but which there was detailed information of the locality of occurrence, were georeferenced through Google Earth Pro and Geoloc tool (available in http://splink.cria.org.br/geoloc).

In this sense, we were able to compile 4,032 occurrence points of amphibian species available in the state of São Paulo. We decided to calibrate our models only in the territorial limit of São Paulo state. We choose this approach for two reasons: first is that due to the large number of gaps in the Neotropical biological database, we would not get the same quantity and quality of data for all the extensions of occurrence of species outside the state of São Paulo. The second reason is that studies showed that under biased and incomplete global sampling regional model performance was not improved (El-Gabbas & Dormann 2018). Besides that, several studies aiming to generate subsidies for conservation planning calibrated their models in a restrict territory and obtained very satisfactory results (e.g., Angeliere et al. 2016, Farashi et al. 2016, El-Gabbas & Dormann 2018, Kalboussi & Achour 2018, Silva et al. 2018).

Predictor variables

Following recommendations on the use of predictor variables relevant to amphibians (Giovanelli et al., in chapter 1 of this thesis), we selected four sets of anurans species based on predictor variables, derived of remote sensing, according to natural history characteristics of the species.

The first group (Group A) contains the species of the genus *Brachycephalus*, notably known in the São Paulo state as species that occur in altitudinal gradients of the Atlantic Forest biome. In this sense, predictor variables related to topographic features are important for the modeling, so we selected slope and elevation as descriptive variables of the steep relief of this region (Table 1). In addition, species in the genus *Brachycephalus* deposits their eggs

directly on the forest litter and it is reasonable to assume that occurrence of forests is an ecologically meaningfull variable for this species; thereby, we selected as predictor variables two types of forest cover of the Atlantic Forest biome: Evergreen Broadleaf Trees and Deciduous Broadleaf Trees (Table 1).

The second group (Group B) contains the species that necessarily require current water courses for reproduction. These species usually live near streams and waterfalls, where they lay their eggs in the water or on the surface of moist rocks. For this grouping we selected slope, distance from rivers, and density of rivers as variables describing the main characteristics of the water bodies used by these species. In addition, we choose a variable related to tropical forest (i.e., Evergreen Broadleaf Trees), since like the genus *Brachycephalus*, these species usually occur mainly in dense ombrophilous forests of the Atlantic Forest biome (Table 1).

The third group (Group C) contains the species that have direct development of eggs or terrestrial larval development. Species of this group are usually found on the forest floor, not associated to water bodies. These species seem to prefer pristine areas, but they are also present in forest fragments (Dixo & Verdade 2006). In this sense, for these species we selected elevation, distance from rivers (make the forest floor wetter and more propitious to reproduction of this group of species), and two types of forest cover of the Atlantic Forest biome (i.e., Evergreen Broadleaf Trees and Deciduous Broadleaf Trees) as variables describing the main characteristics of the habitat used (Table 1).

Finally, the fourth group (Group D) contains generalist species that occur in several environments of São Paulo state. These species inhabit streams, marshes, and temporary ponds, where they also breed. They are also well adapted to anthropogenically altered environments. For these species we generated a topographic wetness index (TWI), which

combines local upslope contributing area and slope, being commonly used to quantify topographic control on hydrological processes (Sørensen & Seibert 2007). Currently, this index has been used as a solution to find the distribution of flash-flood-prone areas (Pourali et al. 2016). For amphibians, the TWI would be a relevant predictor variable to identify wetter areas that could serve as breeding sites for species that have both direct and indirect development, especially those reproducing in lentic water. As predictor variable, we also also selected a type of vegetation cover that represents the open areas where the species occur (i.e., Mixed/Other Trees) (Table 1).

In addition to the predictor variables related to the natural history of amphibians, we also selected a set of climatic variables that was used by all four selected groups. We considered relevant variables for all species, selecting only predictor variables that express seasonality and extreme temperatures and precipitations derived of WorldClim version 2.0 dataset (Table 1). We calculated the correlations among WorldClim version 2.0 and remote sensing variables to exclude the highly correlated ones ($r > 0.75$). All predictor variables have approximately 1 km^2 resolution (in equator region).

Modeling methods

We used four different algorithms to predict the amphibian distribution models: Bioclim (Nix & Busby 1986), Gower (Carpenter et al. 1993), MaxEnt (Phillips et al. 2006), and SVM (Cortes & Vapnik 1995, Drake & Bossenbroek 2009). For each algorithm we ran 10 replicates with 75 % of occurrence for training model and 25 % for model test (10 replicates x 4 algorithms). The algorithms were modeled using “dismo” and “kernlab” R-packages (Hijmans et al. 2015, Karatzoglou et al. 2004).

We used ensemble forecasting (Araújo and New 2007) to determine a consensus map for each species. We estimated “maximum sum of specificity and sensitivity” threshold values

for each generated model, and then binarized the continuous suitability maps (presence or absence). This threshold value is recommended when using presence only algorithms (Liu et al. 2016, Moraes et al. 2019). Also, we evaluated the models based on True Skill Statistic (TSS) values (Allouche et al. 2006) and by the area under the receiver operating characteristic curve (AUC) value, a threshold-independent measure of overall model performance (Fielding and Bell 1997, Manel et al. 2001). Prior to generating the suitability consensus map, all binarized maps were overlapped within the same algorithm and then between algorithms. The consensus maps (referred to as suitability map for each studied species) had suitability values varying from 0 to 40 and after divided by 40, indicating the frequency of models that predicted species presence in each cell. To avoid accuracy errors, we developed models only of species with more than seven points of occurrence.

Table 1. Climatic variables and data derived from remote sensing selected according to the ecology and natural history of the species present in the four groups selected (see text above for details).

	Variables	Source	Original spatial resolution	Group			
				A	B	C	D
Climate	Temperature Seasonality (BIO4)	WorldClim v.2 (Fick & Hijmans 2017)	30 arc-second	X	X	X	X
	Max. Temperature of Warmest Month (BIO 5)			X	X	X	X
	Annual Precipitation (BIO 12)			X	X	X	X
	Precipitation of Driest Month (BIO 14)			X	X	X	X
	Precipitation Seasonality (BIO 15)			X	X	X	X
Remote Sensing	Elevation	Farr et al. 2007	90 m	X		X	
	Slope	Ambdata (Amaral et al. 2013)	90m	X	X		
	Distance from Rivers	Rennó et al. 2008	30 arc-second		X	X	
	Density of Rivers	Ambdata (Amaral et al. 2013)	30 arc-second		X		
	Topographic Wetness Index (TWI)	This study	30 arc-second				X
	Evergreen Broadleaf Trees	Consensus Land Cover (Tuanmu & Jetz 2014)	30 arc-second	X	X	X	
	Deciduous Broadleaf Trees			X			
	Mixed/Other Trees						X

S-SDM

The steps required to build S-SDMs imply an important choice that influences their predictive performance: the application of a threshold to transform the species-distribution models into binary maps to be added together to build the final S-SDM (Benito et al. 2013). In this sense, we combined the predicted ranges of amphibian species using the tree most used threshold criteria: i) lowest presence threshold, ii) 10 % omission-percentage threshold, and iii) 20 % omission-percentage threshold. For example, a 10 % omission-percentage threshold implies that the suitable habitat of the resulting binary map will contain 90 % of the species presence records (Fielding & Bell 1997).

As suggested by Benito et al. (2013), we compared the results of three thresholds in generated species richness and with ground-truth information provided by Vancine et al. (2018). For this, we used the function extract from "raster" R-packages (Hijmans et al. 2015). The Friedman test was used to verify the existence of significant differences between the observed data present in Vancine et al. (2018) with the predict data generated by the S-SDM for each group analyzed (e.g., Sheldon et al. 1996). The results were expressed in violin plot, a graph that synergistically combines the box plot and the density trace (or smoothed histogram) into a single display that reveals the structure found within the data (Hintze & Nelson 1998). After this, we generated species richness map for each group using the threshold value that expressed values similar to those of data set of Vancine et al. (2018). Then, we used zonal statistics to understand the values of richness for the municipalities of São Paulo state (Openshaw 1996).

Coverage of PAs

To evaluate the representation of richness of amphibians in PAs of São Paulo state, we overlapped the current PA network map, obtained in DATAGEO (http://datageo.ambiente.sp.gov.br/), with the richness maps and calculated the percentage located in protected areas. For this, we choose the threshold value that expressed values similar to those of the data set of Vancine et al. (2018) (see item S-SDMs above).

RESULTS

Amphibians of São Paulo State

The compilation of the occurrence data generated a total of 259 species of amphibians distributed in 14 families: Brachycephalidae (24 species), Bufonidae (8 species), Caeciliidae (6 species), Centrolenidae (2 species), Ceratophryidae (1 species), Craugastoridae (4 species), Cycloramphidae (16 species), Hemiphractidae (7 species), Hylidae (92 species), Hylodidae (23 species), Leptodactylidae (41 species), Microhylidae (12 species), Odontophrynidae (11 species), and Phyllomedusidae (12 species) (Appendix 1).

Potential of Richness

Considering only species with more than seven distinct occurrence points and the models of the species that had AUC > 0.7, it was possible to model the potential distribution of 151 amphibian species, being five species of group A, 27 species of group B, 15 species of group C, and 104 species of group D. All the models were better than random models and had significant ($P < 0.05$) AUC mean values > 0.79 in the testing data.

The cells with the highest species richness were concentrated, for all thresholds used, in the region of Serra do Mar and the cells without species were dispersed mainly in central, north, and west regions of the state (Figure 1).

The final species richness map showed that species richness ranged from 0–4 species/km^2 in group A, 0–17 species/km^2 in group B, 0–14 species/km^2 in group C, and 0–68 species/km^2 in group D (Figure 1).

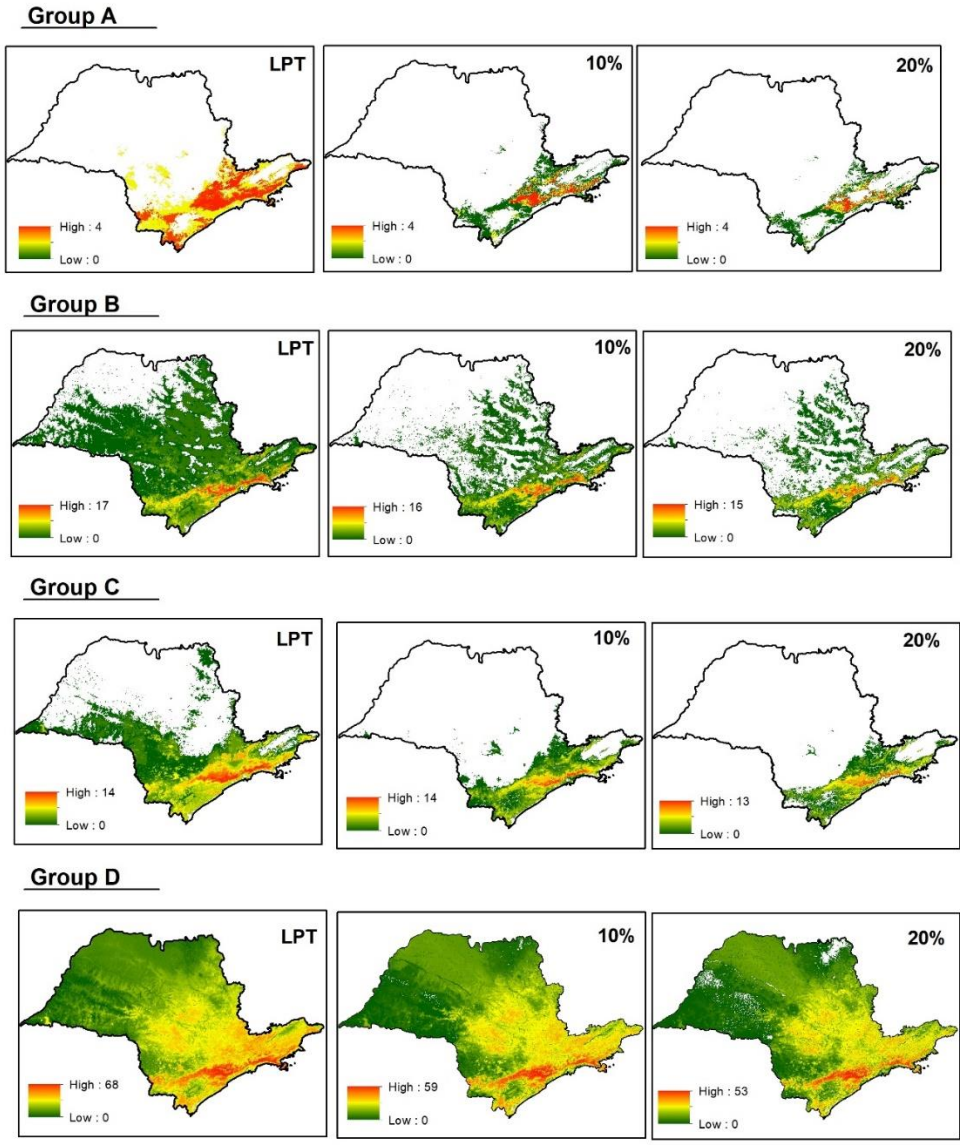

Figure 1. S-SDMs maps showing that species richness (number of species per 1km^2 pixel) ranged from 0–4 species/km^2 in group A, 0–17 species/km^2 in group B, 0–14 species/km^2 in group C, and 0–68 species/km^2 in group D. LPT: lowest presence threshold; 10 %: 10 % omission-percentage threshold, and 20 %: 20 % omission-percentage threshold.

The choice of thresholds

The Friedman test showed that the S-SDMs were similar to the observed data, especially for the 20 % omission-percentage threshold. Only for group B the S-SDM was more similar to the 10 % omission-percentage threshold (Figure 2).

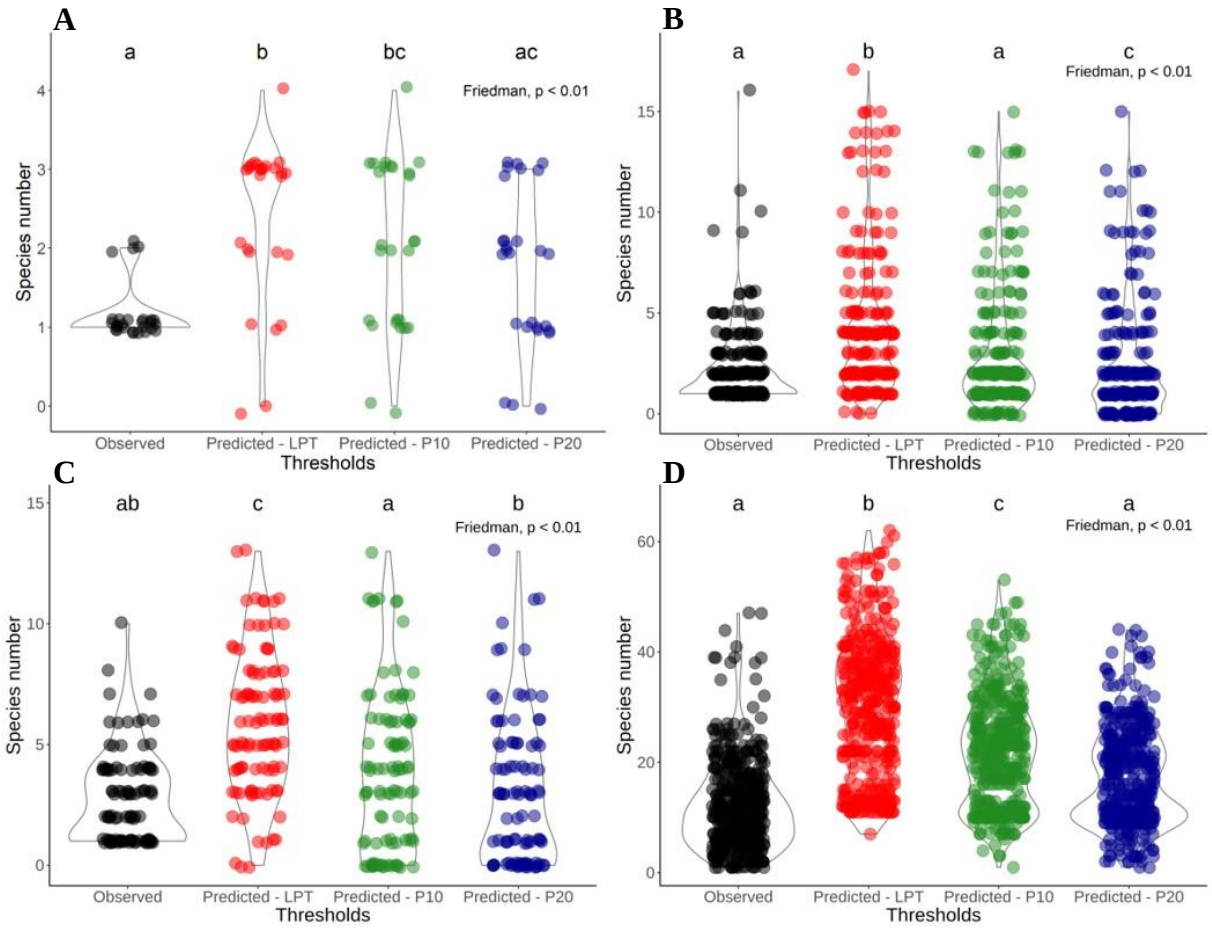

Figure 2. The violin-plot comparison between the observed data and S-SMDs of groups A, B, C, and D. Different letters above each portion indicate significant differences between the mean values of species number. The sequence of letters "ab" above the box-plot indicates that there are no significant differences in the mean values of species number between this portion and the others.

The zonal statistics of the S-SDMs, with the thresholds of 20 % (for groups A, C, and D) and 10 % (for group B), resulted in the quantification of predicted species to occur in each municipality of the state of São Paulo. It was observed that for Group A, the municipalities of the north coast of the state, has large accumulation of species. For group B, C, and D, there is a significant amount of species for the municipalities belonging to the metropolitan region of São Paulo city and the central coastal region (Baixada Santista). For all the groups, the Serra do Mar region was the one with greater accumulation of species of amphibians in São Paulo state (Figure 3).

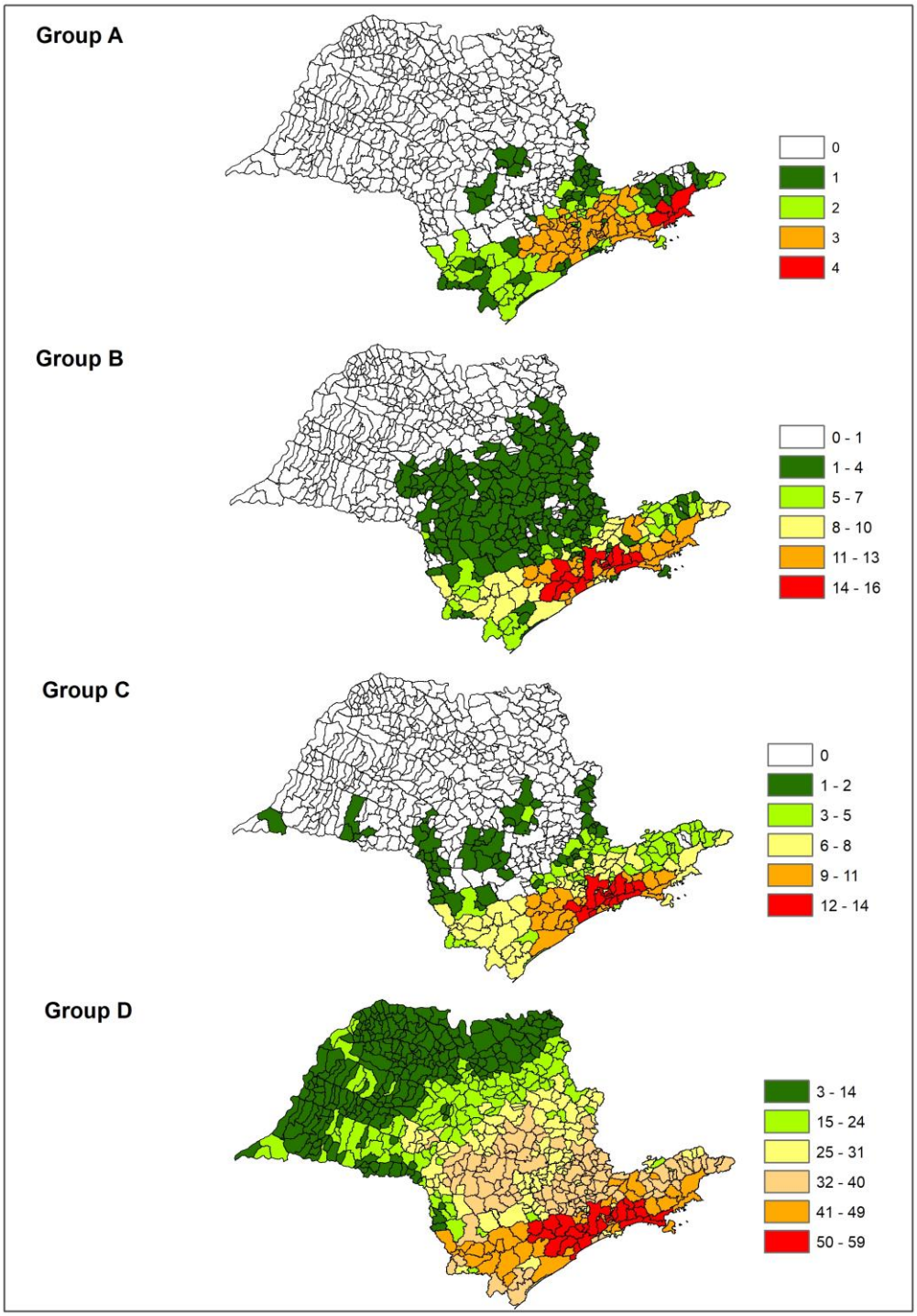

Figure 3. The zonal statistics of the S-SDMs, with the thresholds of 20 % (for groups A, C, and D) and 10 % (for group B), resulted in the spatial quantification of number of predicted species to occur in each municipality of the state of São Paulo

Coverage of PAs

In order to overlap S-SDMs with PAs, again the thresholds of 20 % (for groups A, C, and D) and 10 % (for group B) were used. These thresholds were the ones closest to the observed richness for each group (Figure 4).

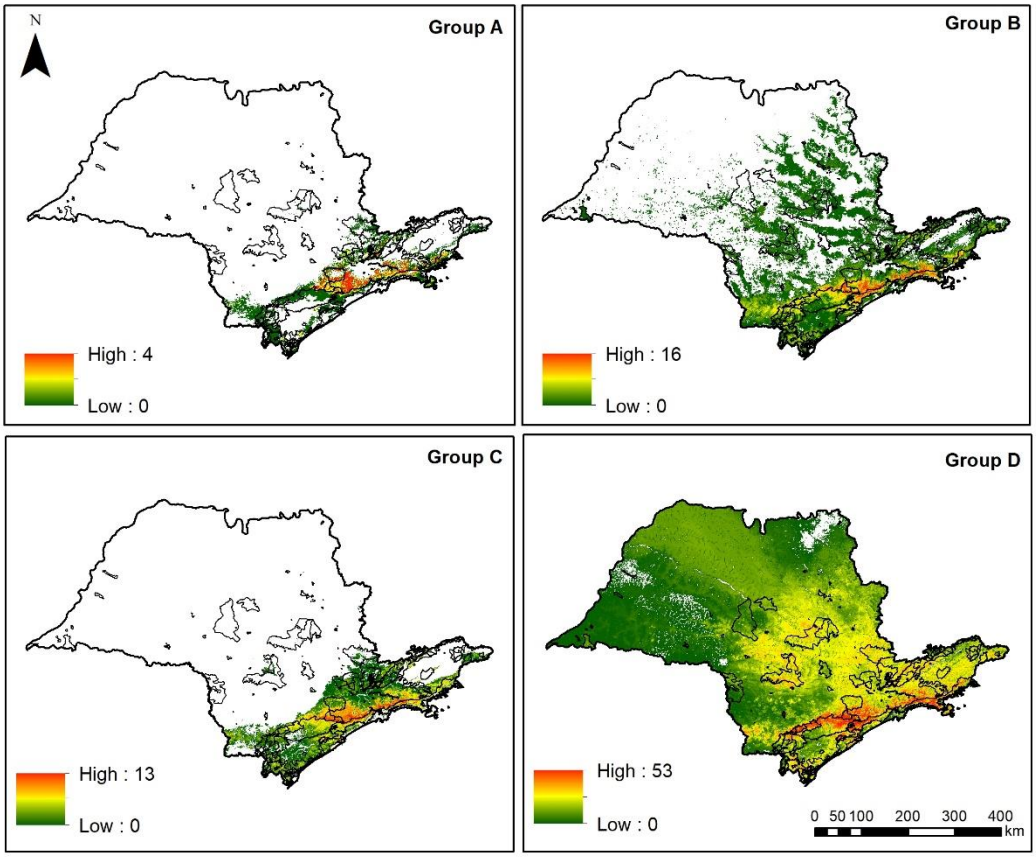

Figure 4. Overlap of the PAs of São Paulo state with the accumulated species richness (number of species per 1km^2 pixel) generated by the S-SDMs of groups A, B, C, and D. Note that the Serra do Mar (red/orange pixels) had the largest accumulation of species for both groups.

Considering the respective IUCN categories of PAs, the categories I, II, V, and VI are those that most cover areas with occurrence predicted by the models. The category I and II (i.e., strict nature reserve and wilderness area) of PAs protect 26.15 % of all occurrence

extension of group A, 9.73 % of group B, 18.77 % of group C, and 3.95 % of group D (Table 2).

Table 2. Percentage of extent of predicted occurrence of groups A, B, C, and D superimposed by IUCN categories of protected areas.

IUCN Protected Areas	Groups			
	A	B	C	D
I - II	26.15 %	9.73 %	18.77 %	3.95 %
III - IV	0.33 %	0.13 %	0.25 %	0.08 %
V - VI	28.73 %	22.30 %	31.42 %	11.12 %

DISCUSSION

The compilation of the occurrence data resulted in an increase of 23 species to the list of amphibians of the state of São Paulo. The last update was made by Rossa-Feres et al. (2011) consisted of 236 species of amphibians. This was due to the fact of the description of new species and the new occurrence of taxa that had not previously occurred in the territory of the state of São Paulo (Appendix 1). As examples of species that increased the list of Rossa-Feres et al. (2011), we can mention *Hylodes japi* (de Sá et al. 2015), *Phrynomedusa dryade* (Baêta et al. 2016), and *Hylodes caete* (Malagoli et al. 2017), recently described and currently considered endemic to the state of São Paulo.

Among the 259 species present in the state of São Paulo, it was only possible to compile the number of points of significant occurrence for 151 species (58 %). This was due to the fact that many species have few known localities, many of which known only from the locality type (see Frost 2018). SDM methods are sensitive to sample size (Wisz et al. 2008) and may not accurately predict habitat distribution patterns for species with few occurrence points (Kumar & Stohlgren 2009). However, the species for which it was possible to run the

models are the most commonly found in several localities, being present in the various inventories already carried out in the state of São Paulo (e.g., Vancine et al. 2018). In addition, these species have a geographical distribution that covers larger areas, occupy different habitats and are susceptible to several anthropic impacts due to their extended distribution.

The fact that Serra do Mar has the largest accumulation of species of the different groups analyzed (i.e., A, B, C, and D) is in agreement with the several studies that show the high potential of species richness of the region (e.g., Condez et al. 2009, Salles et al. 2009, Araujo et al. 2010, Forlani et al. 2010, Garey, Hartmann 2012, Garey et al. 2014, Trevine et al. 2014, Folly et al. 2016). The Serra do Mar is one of the largest mountain ranges in eastern Brazil, stretching for about 1,500 km between the north of the state of Santa Catarina and the north of the state of Rio de Janeiro (Almeida & Carneiro 2017, Gontijo-Pascutti et al. 2012). It is included in the Atlantic Forest biome with altitudes varying from sea level to more than 2,000 m, has varied climatic patterns, great diversity of humid environments, and different vegetal physiognomies (Klein 1984). This environmental heterogeneity contributes to the presence of endemic species of anuran amphibians (Cruz & Feio 2007).

The choice of the threshold was fundamental for the choice of S-SDMs for the different groups of species analyzed. There was a large variation in the predicted richness per pixel among the analyzed thresholds. In this sense, an arbitrary choice of thresholds could result in a significant difference in species (i.e., Group D: LPT = 68 species and 20 % = 53 species). For this study, the 10 % omission-percentage threshold and 20 % omission-percentage threshold are more appropriate for S-SDMs. For other studies that will use S-SDM approach it is desirable to retest the thresholds to verify which ones would be the most appropriate, especially if the same methodology is used for other taxa (e.g., Benito et al. 2013, Calabrese et al. 2014).

Regarding the PAs, the results are satisfactory to predict the occurrence areas of the groups of species analyzed and their overlaps with the different categories of PAs (Dudley 2008). The categories of PAs V and VI (i.e., protected landscape and protected area with sustainable use of natural resources) cover a significant area of the geographic distribution of amphibians. However, the objective of management in these PAs is not strictly biodiversity conservation (Dudley 2008). In this regard, our study shows that efforts could be made to increase the area of effectiveness of the categories of PAs I and II (i.e., strict nature reserve and wilderness area). However, a future analysis of the composition of the species protected by the PAs could provide more meaningful answers to this question.

The results show that the S-SDM approach was effective in capturing the patterns of species richness present in the state of São Paulo. The choice of calibration, made based on the political boundaries of the state of São Paulo, was satisfactory for the geographic scale of analysis (i.e., regional scales). The results of the comparison between field data (e.g., Vancine et al. 2018) and the predicted models showed that for most groups S-SDMs can capture the richness of observed species.

These results may be useful to support environmental planning and selection of priority areas for conservation. For amphibians, these data will be useful to calculate the potential number of species by municipalities, river basins, and PAs (the database of this study will be available at https://anfibiosnomapa.wordpress.com/). Regarding public policies, this study also has great potential to assist in decision making. For example, launched in 2015, the normative instruction of Companhia Ambiental do Estado de São Paulo (CETESB nº 167/2015/C) is still controversial. Although it establishes the obligation of the fauna report assessment, when there is suppression of native vegetation, in the middle and advanced stages of forest regeneration in property above 1,000 m², the regulation establishes sampling efforts according only to the size of the area to be impacted, disregarding standards of richness and

regional endemism. In this sense, our work shows that the amphibian richness can be accessed predictably through the geographic distribution models, helping in the decision making of the choice of the sample effort to be used in fieldwork.

We encourage other researchers to test the same methodology for other taxa in order to expand information on the geographical patterns of biodiversity in the state of São Paulo and other territories.

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Appendix 1. List of species of São Paulo state compiled in databases, and their families and orders. Reference where the species is cited as occurring in the state of São Paulo and the justification for inclusion in the new check list. Group A: genus *Brachycephalus*, B: species that necessarily require current water courses for reproduction, C: species that have direct development of eggs or terrestrial larval development, and D: generalist species that occurs in several environments of São Paulo state. NA: not applicable.

Ordem	Family	Species	Reference	Justification of inclusion	Group
Anura	Brachycephalidae	*Brachycephalus atelopoide*	Frost (2018)	New species	A
Anura	Brachycephalidae	*Brachycephalus crispus*	Frost (2018)	New species	A
Anura	Brachycephalidae	*Brachycephalus ephippium*	Rossa-Feres et al. (2011)	NA	A
Anura	Brachycephalidae	*Brachycephalus guarani*	Frost (2018)	New species	A
Anura	Brachycephalidae	*Brachycephalus hermogenesi*	Rossa-Feres et al. (2011)	NA	A
Anura	Brachycephalidae	*Brachycephalus nodoterga*	Rossa-Feres et al. (2011)	NA	A
Anura	Brachycephalidae	*Brachycephalus pitanga*	Rossa-Feres et al. (2011)	NA	A
Anura	Brachycephalidae	*Brachycephalus sulfuratus*	Frost (2018)	New species	A
Anura	Brachycephalidae	*Brachycephalus toby*	Frost (2018)	New species	A
Anura	Brachycephalidae	*Brachycephalus vertebralis*	Rossa-Feres et al. (2011)	NA	A
Anura	Brachycephalidae	*Ischnocnema bolbodactyla*	Rossa-Feres et al. (2011)	NA	C
Anura	Brachycephalidae	*Ischnocnema gehrti*	Rossa-Feres et al. (2011)	NA	C
Anura	Brachycephalidae	*Ischnocnema guentheri*	Rossa-Feres et al. (2011)	NA	C
Anura	Brachycephalidae	*Ischnocnema hoehnei*	Rossa-Feres et al. (2011)	NA	C
Anura	Brachycephalidae	*Ischnocnema holti*	Rossa-Feres et al. (2011)	NA	C
Anura	Brachycephalidae	*Ischnocnema juipoca*	Rossa-Feres et al. (2011)	NA	C
Anura	Brachycephalidae	*Ischnocnema lactea*	Rossa-Feres et al. (2011)	NA	C
Anura	Brachycephalidae	*Ischnocnema nigriventris*	Rossa-Feres et al. (2011)	NA	C
Anura	Brachycephalidae	*Ischnocnema octavioi*	Frost (2018)	New data of geographic distribution	C
Anura	Brachycephalidae	*Ischnocnema parva*	Rossa-Feres et al. (2011)	NA	C
Anura	Brachycephalidae	*Ischnocnema pusilla*	Rossa-Feres et al. (2011)	NA	C
Anura	Brachycephalidae	*Ischnocnema randorum*	Rossa-Feres et al. (2011)	NA	C
Anura	Brachycephalidae	*Ischnocnema spanios*	Rossa-Feres et al. (2011)	NA	C
Anura	Brachycephalidae	*Ischnocnema vizottoi*	Frost (2018)	New species	C
Anura	Bufonidae	*Dendrophryniscus brevipollicatus*	Rossa-Feres et al. (2011)	NA	D
Anura	Bufonidae	*Dendrophryniscus leucomystax*	Rossa-Feres et al. (2011)	NA	D
Anura	Bufonidae	*Melanophryniscus moreirae*	Rossa-Feres et al. (2011)	NA	B
Anura	Bufonidae	*Rhinella hoogmoedi*	Rossa-Feres et al. (2011)	NA	B

Anura	Bufonidae	*Rhinella icterica*	Rossa-Feres et al. (2011)	NA	B
Anura	Bufonidae	*Rhinella ornata*	Rossa-Feres et al. (2011)	NA	B
Anura	Bufonidae	*Rhinella rubescens*	Rossa-Feres et al. (2011)	NA	D
Anura	Bufonidae	*Rhinella schneideri*	Rossa-Feres et al. (2011)	NA	D
Gymnophiona	Caeciliidae	*Luetkenotyphlus brasiliensis*	Rossa-Feres et al. (2011)	NA	NA
Gymnophiona	Caeciliidae	*Microcaecilia supernumeraria*	Rossa-Feres et al. (2011)	NA	NA
Gymnophiona	Caeciliidae	*Siphonops annulatus*	Rossa-Feres et al. (2011)	NA	NA
Gymnophiona	Caeciliidae	*Siphonops hardyi*	Rossa-Feres et al. (2011)	NA	NA
Gymnophiona	Caeciliidae	*Siphonops insulanus*	Rossa-Feres et al. (2011)	NA	NA
Gymnophiona	Caeciliidae	*Siphonops paulensis*	Rossa-Feres et al. (2011)	NA	NA
Anura	Centrolenidae	*Vitreorana eurygnatha*	Rossa-Feres et al. (2011)	NA	B
Anura	Centrolenidae	*Vitreorana uranoscopa*	Rossa-Feres et al. (2011)	NA	B
Anura	Ceratophryidae	*Ceratophrys aurita*	Rossa-Feres et al. (2011)	NA	D
Anura	Craugastoridae	*Barycholos ternetzi*	Rossa-Feres et al. (2011)	NA	C
Anura	Craugastoridae	*Haddadus binotatus*	Rossa-Feres et al. (2011)	NA	C
Anura	Craugastoridae	*Holoaden luederwaldti*	Rossa-Feres et al. (2011)	NA	C
Anura	Craugastoridae	*Holoaden suarezi*	Frost (2018)	New species	C
Anura	Cycloramphidae	*Cycloramphus acangatan*	Rossa-Feres et al. (2011)	NA	C
Anura	Cycloramphidae	*Cycloramphus boraceiensis*	Rossa-Feres et al. (2011)	NA	B
Anura	Cycloramphidae	*Cycloramphus carvalhoi*	Rossa-Feres et al. (2011)	NA	B
Anura	Cycloramphidae	*Cycloramphus dubius*	Rossa-Feres et al. (2011)	NA	B
Anura	Cycloramphidae	*Cycloramphus eleutherodactylus*	Rossa-Feres et al. (2011)	NA	C
Anura	Cycloramphidae	*Cycloramphus faustoi*	Rossa-Feres et al. (2011)	NA	B
Anura	Cycloramphidae	*Cycloramphus granulosus*	Rossa-Feres et al. (2011)	NA	B
Anura	Cycloramphidae	*Cycloramphus izecksohni*	Rossa-Feres et al. (2011)	NA	B
Anura	Cycloramphidae	*Cycloramphus juimirim*	Rossa-Feres et al. (2011)	NA	B
Anura	Cycloramphidae	*Cycloramphus lutzorum*	Rossa-Feres et al. (2011)	NA	B
Anura	Cycloramphidae	*Cycloramphus semipalmatus*	Rossa-Feres et al. (2011)	NA	B
Anura	Cycloramphidae	*Cycloramphus stejnegeri*	Rossa-Feres et al. (2011)	NA	B
Anura	Cycloramphidae	*Thoropa miliaris*	Rossa-Feres et al. (2011)	NA	B
Anura	Cycloramphidae	*Thoropa petropolitana*	Rossa-Feres et al. (2011)	NA	B
Anura	Cycloramphidae	*Thoropa taophora*	Rossa-Feres et al. (2011)	NA	B
Anura	Cycloramphidae	*Zachaenus parvulus*	Rossa-Feres et al.	NA	C

			(2011)		
Anura	Hemiphractidae	*Fritziana fissilis*	Rossa-Feres et al. (2011)	NA	D
Anura	Hemiphractidae	*Fritziana goeldii*	Rossa-Feres et al. (2011)	NA	NA
Anura	Hemiphractidae	*Fritziana ohausi*	Rossa-Feres et al. (2011)	NA	D
Anura	Hemiphractidae	*Fritziana ulei*	Frost (2018)	New data of geographic distribution	NA
Anura	Hemiphractidae	*Gastrotheca albolineata*	Rossa-Feres et al. (2011)	NA	NA
Anura	Hemiphractidae	*Gastrotheca fulvorufa*	Frost (2018)	Removed from the synonymy of *Gastrotheca microdiscus*	NA
Anura	Hemiphractidae	*Gastrotheca microdiscus*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Aparasphenodon bokermanni*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Aparasphenodon brunoi*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Aplastodiscus albofrenatus*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Aplastodiscus albosignatus*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Aplastodiscus arildae*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Aplastodiscus callipygius*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Aplastodiscus ehrhardti*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Aplastodiscus eugenioi*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Aplastodiscus leucopygius*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Aplastodiscus perviridis*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Boana albomarginata*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Boana albopunctata*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Boana bandeirantes*	Frost (2018)	New species	D
Anura	Hylidae	*Boana bischoffi*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Boana caingua*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Boana caipora*	Rossa-Feres et al. (2011)	NA	B
Anura	Hylidae	*Boana cymbalum*	Rossa-Feres et al. (2011)	NA	B
Anura	Hylidae	*Boana faber*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Boana latistriata*	Rossa-Feres et al. (2011)	NA	B
Anura	Hylidae	*Boana lundii*	Rossa-Feres et al. (2011)	NA	B
Anura	Hylidae	*Boana pardalis*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Boana polytaena*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Boana prasina*	Rossa-Feres et al.	NA	D

			(2011)		
Anura	Hylidae	*Boana punctata*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Boana raniceps*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Boana semilineata*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Bokermannohyla ahenea*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Bokermannohyla astartea*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Bokermannohyla circumdata*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Bokermannohyla claresignata*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Bokermannohyla clepsydra*	Rossa-Feres et al. (2011)	NA	NA
Anura	Hylidae	*Bokermannohyla hylax*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Bokermannohyla izecksohni*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Bokermannohyla luctuosa*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Dendropsophus anceps*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Dendropsophus berthalutzae*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Dendropsophus decipiens*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Dendropsophus elegans*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Dendropsophus elianeae*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Dendropsophus giesleri*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Dendropsophus jimi*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Dendropsophus limai*	Rossa-Feres et al. (2011)	NA	NA
Anura	Hylidae	*Dendropsophus microps*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Dendropsophus minutus*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Dendropsophus nanus*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Dendropsophus rhea*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Dendropsophus rubicundulus*	Frost (2018)	NA	D
Anura	Hylidae	*Dendropsophus sanborni*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Dendropsophus seniculus*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Dendropsophus werneri*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Itapotihyla langsdorffii*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Ololygon alcatraz*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Ololygon angrensis*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Ololygon argyreornata*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Ololygon ariadne*	Rossa-Feres et al.	NA	B

			(2011)		
Anura	Hylidae	*Ololygon atrata*	Rossa-Feres et al. (2011)	NA	B
Anura	Hylidae	*Ololygon berthae*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Ololygon brieni*	Rossa-Feres et al. (2011)	NA	B
Anura	Hylidae	*Ololygon caissara*	Frost (2018)	New species	B
Anura	Hylidae	*Ololygon canastrensis*	Rossa-Feres et al. (2011)	NA	B
Anura	Hylidae	*Ololygon faivovichi*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Ololygon flavoguttata*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Ololygon hiemalis*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Ololygon jureia*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Ololygon littoralis*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Ololygon obtriangulata*	Rossa-Feres et al. (2011)	NA	B
Anura	Hylidae	*Ololygon peixotoi*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Ololygon perpusilla*	Rossa-Feres et al. (2011)	NA	B
Anura	Hylidae	*Ololygon rizibilis*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Pseudis platensis*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Scinax alter*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Scinax caldarum*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Scinax crospedospilus*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Scinax duartei*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Scinax eurydice*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Scinax fuscomarginatus*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Scinax fuscovarius*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Scinax hayii*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Scinax imbegue*	Frost (2018)	New species	D
Anura	Hylidae	*Scinax nasicus*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Scinax perereca*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Scinax similis*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Scinax squalirostris*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Scinax tymbamirim*	Frost (2018)	New species	D
Anura	Hylidae	*Scinax x-signatus*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Sphaenorhynchus caramaschii*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Sphaenorhynchus orophilus*	Rossa-Feres et al. (2011)	NA	D

Anura	Hylidae	*Trachycephalus imitatrix*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Trachycephalus lepidus*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Trachycephalus mesophaeus*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Trachycephalus nigromaculatus*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylidae	*Trachycephalus typhonius*	Rossa-Feres et al. (2011)	NA	D
Anura	Hylodidae	*Crossodactylus boulengeri*	Frost (2018)	Revalidation	B
Anura	Hylodidae	*Crossodactylus caramaschii*	Rossa-Feres et al. (2011)	NA	B
Anura	Hylodidae	*Crossodactylus dispar*	Rossa-Feres et al. (2011)	NA	B
Anura	Hylodidae	*Crossodactylus gaudichaudii*	Rossa-Feres et al. (2011)	NA	B
Anura	Hylodidae	*Crossodactylus grandis*	Rossa-Feres et al. (2011)	NA	B
Anura	Hylodidae	*Crossodactylus werneri*	Frost (2018)	New species	B
Anura	Hylodidae	*Hylodes asper*	Rossa-Feres et al. (2011)	NA	B
Anura	Hylodidae	*Hylodes caete*	Frost (2018)	New species	B
Anura	Hylodidae	*Hylodes cardosoi*	Rossa-Feres et al. (2011)	NA	B
Anura	Hylodidae	*Hylodes dactylocinus*	Rossa-Feres et al. (2011)	NA	B
Anura	Hylodidae	*Hylodes heyeri*	Rossa-Feres et al. (2011)	NA	B
Anura	Hylodidae	*Hylodes japi*	Frost (2018)	New species	B
Anura	Hylodidae	*Hylodes magalhaesi*	Rossa-Feres et al. (2011)	NA	B
Anura	Hylodidae	*Hylodes mertensi*	Rossa-Feres et al. (2011)	NA	B
Anura	Hylodidae	*Hylodes nasus*	Rossa-Feres et al. (2011)	NA	B
Anura	Hylodidae	*Hylodes ornatus*	Rossa-Feres et al. (2011)	NA	B
Anura	Hylodidae	*Hylodes phyllodes*	Rossa-Feres et al. (2011)	NA	B
Anura	Hylodidae	*Hylodes sazimai*	Rossa-Feres et al. (2011)	NA	B
Anura	Hylodidae	*Megaelosia bocainensis*	Rossa-Feres et al. (2011)	NA	B
Anura	Hylodidae	*Megaelosia boticariana*	Rossa-Feres et al. (2011)	NA	B
Anura	Hylodidae	*Megaelosia goeldii*	Rossa-Feres et al. (2011)	NA	B
Anura	Hylodidae	*Megaelosia jordanensis*	Rossa-Feres et al. (2011)	NA	B
Anura	Hylodidae	*Megaelosia massarti*	Rossa-Feres et al. (2011)	NA	B
Anura	Leptodactylidae	*Adenomera ajurauna*	Rossa-Feres et al. (2011)	NA	C
Anura	Leptodactylidae	*Adenomera bokermanni*	Rossa-Feres et al. (2011)	NA	C
Anura	Leptodactylidae	*Adenomera marmorata*	Rossa-Feres et al. (2011)	NA	C
Anura	Leptodactylidae	*Adenomera thomei*	Ferrante et al. (2014)	NA	C
Anura	Leptodactylidae	*Leptodactylus chaquensis*	Rossa-Feres et al. (2011)	NA	D

Anura	Leptodactylidae	*Leptodactylus flavopictus*	Rossa-Feres et al. (2011)	NA	D
Anura	Leptodactylidae	*Leptodactylus furnarius*	Rossa-Feres et al. (2011)	NA	D
Anura	Leptodactylidae	*Leptodactylus fuscus*	Rossa-Feres et al. (2011)	NA	D
Anura	Leptodactylidae	*Leptodactylus jolyi*	Rossa-Feres et al. (2011)	NA	D
Anura	Leptodactylidae	*Leptodactylus labyrinthicus*	Rossa-Feres et al. (2011)	NA	D
Anura	Leptodactylidae	*Leptodactylus latrans*	Rossa-Feres et al. (2011)	NA	D
Anura	Leptodactylidae	*Leptodactylus mystaceus*	Rossa-Feres et al. (2011)	NA	D
Anura	Leptodactylidae	*Leptodactylus mystacinus*	Rossa-Feres et al. (2011)	NA	D
Anura	Leptodactylidae	*Leptodactylus notoaktites*	Rossa-Feres et al. (2011)	NA	D
Anura	Leptodactylidae	*Leptodactylus podicipinus*	Rossa-Feres et al. (2011)	NA	D
Anura	Leptodactylidae	*Leptodactylus sertanejo*	Rossa-Feres et al. (2011)	NA	D
Anura	Leptodactylidae	*Leptodactylus syphax*	Rossa-Feres et al. (2011)	NA	D
Anura	Leptodactylidae	*Paratelmatobius cardosoi*	Rossa-Feres et al. (2011)	NA	D
Anura	Leptodactylidae	*Paratelmatobius gaigeae*	Rossa-Feres et al. (2011)	NA	D
Anura	Leptodactylidae	*Paratelmatobius mantiqueira*	Rossa-Feres et al. (2011)	NA	D
Anura	Leptodactylidae	*Paratelmatobius poecilogaster*	Rossa-Feres et al. (2011)	NA	D
Anura	Leptodactylidae	*Paratelmatobius yepiranga*	Rossa-Feres et al. (2011)	NA	D
Anura	Leptodactylidae	*Physalaemus atlanticus*	Rossa-Feres et al. (2011)	NA	D
Anura	Leptodactylidae	*Physalaemus barrioi*	Rossa-Feres et al. (2011)	NA	D
Anura	Leptodactylidae	*Physalaemus bokermanni*	Rossa-Feres et al. (2011)	NA	D
Anura	Leptodactylidae	*Physalaemus centralis*	Rossa-Feres et al. (2011)	NA	D
Anura	Leptodactylidae	*Physalaemus cuvieri*	Rossa-Feres et al. (2011)	NA	D
Anura	Leptodactylidae	*Physalaemus jordanensis*	Rossa-Feres et al. (2011)	NA	D
Anura	Leptodactylidae	*Physalaemus lateristriga*	Frost (2018)	Revalidation	D
Anura	Leptodactylidae	*Physalaemus maculiventris*	Rossa-Feres et al. (2011)	NA	D
Anura	Leptodactylidae	*Physalaemus marmoratus*	Rossa-Feres et al. (2011)	NA	D
Anura	Leptodactylidae	*Physalaemus moreirae*	Rossa-Feres et al. (2011)	NA	D
Anura	Leptodactylidae	*Physalaemus nattereri*	Rossa-Feres et al. (2011)	NA	D
Anura	Leptodactylidae	*Physalaemus olfersii*	Rossa-Feres et al. (2011)	NA	D
Anura	Leptodactylidae	*Physalaemus signifer*	Rossa-Feres et al. (2011)	NA	D
Anura	Leptodactylidae	*Physalaemus spiniger*	Rossa-Feres et al. (2011)	NA	D
Anura	Leptodactylidae	*Pseudopaludicola atragula*	Frost (2018)	New species	D
Anura	Leptodactylidae	*Pseudopaludicola falcipes*	Rossa-Feres et al. (2011)	NA	D

Anura	Leptodactylidae	*Pseudopaludicola murundu*	Rossa-Feres et al. (2011)	NA	D
Anura	Leptodactylidae	*Pseudopaludicola mystacalis*	Rossa-Feres et al. (2011)	NA	D
Anura	Leptodactylidae	*Pseudopaludicola saltica*	Rossa-Feres et al. (2011)	NA	D
Anura	Microhylidae	*Arcovomer passarellii*	Rossa-Feres et al. (2011)	NA	D
Anura	Microhylidae	*Chiasmocleis albopunctata*	Rossa-Feres et al. (2011)	NA	D
Anura	Microhylidae	*Chiasmocleis altomontana*	Frost (2018)	New species	D
Anura	Microhylidae	*Chiasmocleis atlantica*	Rossa-Feres et al. (2011)	NA	D
Anura	Microhylidae	*Chiasmocleis lacrimae*	Frost (2018)	New species	D
Anura	Microhylidae	*Chiasmocleis leucosticta*	Rossa-Feres et al. (2011)	NA	D
Anura	Microhylidae	*Chiasmocleis mantiqueira*	Rossa-Feres et al. (2011)	NA	D
Anura	Microhylidae	*Dermatonotus muelleri*	Rossa-Feres et al. (2011)	NA	D
Anura	Microhylidae	*Elachistocleis bicolor*	Rossa-Feres et al. (2011)	NA	D
Anura	Microhylidae	*Elachistocleis cesarii*	Rossa-Feres et al. (2011)	NA	D
Anura	Microhylidae	*Myersiella microps*	Rossa-Feres et al. (2011)	NA	D
Anura	Microhylidae	*Stereocyclops parkeri*	Rossa-Feres et al. (2011)	NA	D
Anura	Odontophrynidae	*Macrogenioglottus alipioi*	Rossa-Feres et al. (2011)	NA	D
Anura	Odontophrynidae	*Odontophrynus americanus*	Rossa-Feres et al. (2011)	NA	D
Anura	Odontophrynidae	*Odontophrynus cultripes*	Rossa-Feres et al. (2011)	NA	D
Anura	Odontophrynidae	*Proceratophrys appendiculata*	Rossa-Feres et al. (2011)	NA	D
Anura	Odontophrynidae	*Proceratophrys belzebul*	Frost (2018)	New species	D
Anura	Odontophrynidae	*Proceratophrys boiei*	Rossa-Feres et al. (2011)	NA	D
Anura	Odontophrynidae	*Proceratophrys gladius*	Frost (2018)	New species	D
Anura	Odontophrynidae	*Proceratophrys itamari*	Frost (2018)	New species	D
Anura	Odontophrynidae	*Proceratophrys melanopogon*	Rossa-Feres et al. (2011)	NA	D
Anura	Odontophrynidae	*Proceratophrys moratoi*	Rossa-Feres et al. (2011)	NA	D
Anura	Odontophrynidae	*Proceratophrys pombali*	Frost (2018)	New species	D
Anura	Phyllomedusidae	*Phasmahyla cochranae*	Rossa-Feres et al. (2011)	NA	B
Anura	Phyllomedusidae	*Phasmahyla guttata*	Rossa-Feres et al. (2011)	NA	B
Anura	Phyllomedusidae	*Phrynomedusa bokermanni*	Rossa-Feres et al. (2011)	NA	B
Anura	Phyllomedusidae	*Phrynomedusa dryade*	Frost (2018)	New species	B
Anura	Phyllomedusidae	*Phrynomedusa fimbriata*	Rossa-Feres et al. (2011)	NA	B
Anura	Phyllomedusidae	*Phrynomedusa vanzolinii*	Rossa-Feres et al. (2011)	NA	B
Anura	Phyllomedusidae	*Phyllomedusa ayeaye*	Rossa-Feres et al. (2011)	NA	D
Anura	Phyllomedusidae	*Phyllomedusa azurea*	Rossa-Feres et al. (2011)	NA	D

Anura	Phyllomedusidae	*Phyllomedusa burmeisteri*	Rossa-Feres et al. (2011)	NA	D
Anura	Phyllomedusidae	*Phyllomedusa distincta*	Rossa-Feres et al. (2011)	NA	D
Anura	Phyllomedusidae	*Phyllomedusa rohdei*	Rossa-Feres et al. (2011)	NA	D
Anura	Phyllomedusidae	*Phyllomedusa tetraploidea*	Rossa-Feres et al. (2011)	NA	D

Capítulo 3

Remotely sensed variables predict the potential distribution of an alien amphibian **Eleutherodactylus johnstonei** *(Anura: Eleutherodactylidae) in Brazil*

ORIGINAL ARTICLE

Remotely sensed variables predict the potential distribution of an alien amphibian *Eleutherodactylus johnstonei* (Anura: Eleutherodactylidae) in Brazil

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Abstract

Eleutherodactylus johnstonei is a frog native of the Lesser Antilles introduced in Brazil in the mid of 1990s. So far, the population is restricted to urban areas in the São Paulo city. However, due to it is feasible success for new colonization we presented a modeling framework to predict the potential distribution of this alien invasive species in Brazil. Here, we used MAXENT algorithm (i) to model the native geographic distribution of *E. jonshtonei* and (ii) to project that model to the whole of Brazil. We used predictors variables derived from remote sensing that improve model performance at regional scales. Temperature annual range (20.1%); annual precipitation (18.7%); cultivated and managed vegetation (16.7%); and bare soil (11.5%) were the main variables contributing for the distribution model for *E. johnstonei*. The model projection in Brazil showed greater potential of invasion in disturbed habitats. Furthermore, the suitability of *E. johnstonei* increased near the cities and roads, being a concern way of dispersion. *E. johnstonei* is the first species of amphibian that has the potential to cause socioeconomic impacts in Brazil, such as transmission of infectious diseases, diseases linked to sleep, and depreciation in real estate value. The present study can support management actions for controlling and avoiding the species establishment of the new populations in areas with predicted occurrences.

Keywords: Anura, Biological invasion, Decision-making, EarthEnv, Exotic species, MAXENT, Socioeconomic impacts

INTRODUCTION

Biological invasion is one of the most important causes of biodiversity loss (Mollot et al. 2017). Invasive species may change the communities' structure and consequently the ecosystem function due to the transfer of pathogens and parasites, and the alterations in the ecological interactions between native species (e.g. Dowding and Murphy 2001, Hatcher et al. 2012, Hegel and Marini 2013). A successful colonization of an invasive species depends on intrinsic traits such a broad physiological and ecological plasticity, as well as abiotic factors such as appropriated climate, and availability of essential resources (Mack 1996, Thuiller et al. 2005, Both et al. 2014).

In the last decades, many studies report the presence of invasive species of amphibians in different parts of the world (e.g. Lowe et al. 2000, Kats and Ferrer 2003, Kraus 2009, Kraus 2015). Most notorious invasive species are the American Bullfrog (*Lithobates catesbeianus*) and Cane Toad (*Rhinella marina*). Both of them have been translocated intentionally to a dozen of countries worldwide (Lever 2001, Kraus 2009, Lever 2003, Ficetola et al. 2007). However, the reasons are different because the American Bullfrog (native from east of North America) was a food source for humans (Liu and Li 2009), and Cane Toad (native from South and Central Americas) was an attempt to control agricultural pests (Lever 2001). Both species share history-life traits that make them successful invaders such as huge size, high fecundity, and high locomotor performance favoring the expansion to novel environments (Li et al 2014). The negative impacts of the Bullfrog and Cane Toad on native species/populations of amphibians are declines and extinctions (Brunett 1997, Murray and Hose 2005), predation (Kats and Ferrer 2003, Boland 2004, Silva et al. 2011), competition (Kiesecker et al. 2001, Blaustein and Kiesecker 2002), interference in vocalizations parameters (Both and Grant

2012, Bleach et al. 2015) and, vector of disease and parasites (Schloegel et al. 2010, Liu et al. 2013).

Some species of the genus *Eleutherodactylus* are also successful invaders, but not all species are considered invasive but only alien because the ecological and socio-economic impacts were not detected. On the contrary of the Bullfrog and Cane toad, *Eleutherodactylus* species are small sized and low fecundity (Crawford and Smith, 2005). However, some life-history traits such as direct development, high physiological tolerance and generalist diet favoring the rapid adaptability to novel environments (Pough et al. 1977, Kaiser 1997). The best-known species is *Eleutherodactylus coqui*, introduced in Hawai in the 1980s, and frequently find in high densities in different types of vegetation and altitudes (Bisrat et al. 2011). Currently, it causes substantial damages to the economy due to the noise resulted in the calls (Kaiser and Burnett 2006).

Until recently, the American Bullfrog (*Lithobates catesbeianus*) was considered the only non-native invasive species of amphibian in Brazil (Giovanelli et al. 2008). However, in 2012 another non-native invasive terrestrial frog was found in Southeastern Brazil, particularly in the São Paulo city (Melo et al. 2014). This species was identified as *Eleutherodactylus johnstonei*, a frog native of Lesser Antilles islands (Schwartz 1967) by barcoding molecular techniques and morphology (Melo et al. 2014). This species has a direct development, generalist food habit, and broad environmental tolerances; it was introduced in other countries of Latin America like Colombia, Venezuela, and Guianas (Kaiser 1997). In Brazil, the population of *E. johnstonei* occurs in the gardens and yards of the houses and, as its congeneric *Eleutherodactylus coqui* in Hawaii (Bisrat et al. 2012), disturbes the sleep of residents by the loud vocalizations, causing troubles to the wildlife management agency of the São Paulo government. Until now, *E. johnstonei* remained close to the region where it was probably first introduced. However, as this species fits well in heavily anthropogenic

disturbed habitats (Bomford et al. 2009), there is concern if the species will be able to spread in other regions of São Paulo state and Brazil and even invading the Atlantic rainforest biodiversity hotspot.

Species distribution modeling (SDM) is a powerful tool to assess potential geographic distributions of species (Guisan and Thuiller 2005, Elith et al. 2006), providing information for conservation planning strategies (Guisan et al. 2013). SDM has also been applied to the prediction of the invasive potential of non-native species (Peterson and Vieglais 2001, Peterson et al. 2003, Papes and Peterson 2003, Ficetola et al. 2007, Rodder and Lotters, 2010), including the actual distribution of the *Lithobates catesbeianus* in Brazil (Giovanelli et al. 2008). Currently, plethora of remotely sensed products as Moderate Resolution Imaging Spectroradiometer (MODIS) can be used in SDM improving model performance at regional scales. This data is continuously observed without interpolation and geographical biases. Therefore, satellite-based temperature, precipitation and radiation measurements could improve climate predictor variables. Even, remotely sensed metrics condition, such as the normalized different vegetation index (NDVI) and leaf area index (LAI), both effective proxies for vegetation productivity, can be used as habitat predictors (He et al. 2015).

Detailed studies with GIS technology are necessary to know the potential geographic distribution of *Eleutherodactylus johnstonei* in Brazil and to support actions of contention and eradication of this species (Melo et al. 2014). In this sense, the aim of our study was to examine whether the remotely sensed variables are efficient to generate a predictive map for the distribution of this species in Brazil. First, we developed a SDM-based methodology to model the native geographic distribution of *E. johnstonei* in Lesser Antilles using remote sensing-based predictors, mainly land cover, precipitation, and temperature. Second, we projected this model using the same predictor variables to Brazil

MATERIAL AND METHODS

Occurrence data

To predict the potential distribution of *Eleutherodactylus johnstonei* we took 132 georeferenced occurrence points in Lesser Antilles from the Global Biodiversity Information Facility database - GBIF (http://www.gbif.org, accessed on 11/22/2016). After, considering Kaiser (1997), we took only native localities of *E. johnstonei*. This dataset was checked in the DIVA-GIS software (Hijmans et al. 2002) for bias and errors and resulted in 26 selected occurrence points fitness for use (e.g., Chapman 2005).

Environmental data

We compiled the remotely sensed variables in the database of EarthEnv (available at https://www.earthenv.org/) and Worldclim version 2 (available at http://worldclim.org/version2). The EarthEnv project is a global remote-sensing supported by environmental layers for assessing status and trends in biodiversity, ecosystems, and climate. It is a collaborative project of biodiversity scientists and remote sensing experts to develop near-global standardized layers with ~1 km resolution for monitoring and modeling biodiversity (Earthenv 2018). In this database we choose the predictor variables of the Global 1-km Consensus Land Cover dataset. This dataset integrates multiple global remote sensing-derived land-cover products and provide consensus information on the prevalence of 12 land-cover classes at 1-km resolution. We used the full version of this dataset integrating GlobCover (2005-06; v2.2), the MODIS land-cover product (MCD12Q1; v051), GLC2000 (global product; v1.1), and DISCover (GLCC; v2) (Tuanmu and Jetz 2014).

We used the Bioclim dataset available in the database of WorldClim version 2, with ~1 km resolution. Although using interpolated data, weather station data were interpolated with covariates including elevation, distance to the coast, and three satellite-derived

covariates: maximum and minimum land surface temperature as well as cloud cover, obtained with the MODIS satellite platform (Fick and Hijmans 2017).

To determine which variables to include, we identified redundant environmental layers via SDMToolbox v1.1c of ArcGIS 10.2 in "Remove Highly Correlated Variable" function (Brown 2014). We considered redundant variables showing a correlation Pearson's $r > 0.80$ (Giovanelli et al. 2010). Subsequently, we used four bioclimatic variables and six consensus land cover products (Table 1). All variables had the same spatial extension and spatial resolution of 30 arc-seconds (~ 1 km), with Datum WGS84.

Table 1. Predictor variables used to produce a potential distribution of *Eleutherodactylus johnstonei* in Brazil.

Source	Dataset	Predictor variables	References
Worlclim 2	Bioclim	Max. Temperature of Warmest Month (Bio5) Temperature Annual Range (Bio7) Annual Precipitation (Bio12) Precipitation Seasonality (Bio15)	Fick and Hijmans (2017)
EarthEnv	Consensus land cover	Mixed/other trees (Class 4) Shrubs (Class 5) Herbaceous vegetation (Class 6) Cultivated and managed vegetation (Class 7) Regularly flooded vegetation (Class 8) Bare soil (Class 11)	Tuanmu and Jetz (2014)

Modeling Framework

To produce a potential distribution of *Eleutherodactylus johnstonei* in Brazil, we used the Maxent algorithm (version 3.4.1) (MAXENT; Phillips et al. 2006, software available at https://biodiversityinformatics.amnh.org/open_source/maxent/) that fit with limited presence-

only and pseudo-absences data, providing robust estimates of habitat suitability for invasive species on the landscape (West et al. 2016).

As model parameters in Maxent, we used 500 iterations, 5,000 background points, auto features, random seed, analysis of variable importance, and response curves. We used replicated run type bootstrap to create 10 random partitions from our full locality dataset. Each partition consisted of 75 % of the dataset used for SDM calibration (training), with the other 25 % used for model evaluation (testing). After this, the result was an average model of these 10 partitions.

The logistic output resulted in an average model with values ranging from 0 (unsuitable) to 1 (suitable) (Phillips et al. 2006). We evaluated the average model by the area under the receiver operating characteristic curve (AUC) value, a threshold-independent measure of overall model performance (mean ± standard deviation) (Fielding and Bell 1997; Manel et al. 2001). The AUC is a measure of the area under the ROC ranging from 0.5 (random accuracy) to a maximum value of 1.0 (perfect discrimination) (Fielding and Bell 1997). We also evaluated omission errors and model significance by binomial probability associated to the threshold used.

Following Giovanelli et al. (2008), we projected the result of the average model developed in the Lesser Antilles extent to assess the potential geographic distribution of *Eleutherodactylus johnstone*i in Brazil.

Predictive occurrence, distance of roads and urban areas, and land use

To verify the preference of habitat of *Eleutherodactylus johnstonei* in Brazil, we used Spatial Analyst Tools in GRASS GIS 7.4 to extract the potential occurrence in Brazil. After this, we intersected this information with land use map, obtained in Global Land Cover, available for the year 2014

(http://www.fao.org/geonetwork/srv/en/metadata.show?uuid=ba4526fd-cdbf-4028-a1bd-5a559c4bff38&currTab=distribution).

To understand the relation between habitat suitability of *Eleutherodactylus johnstonei* and distance of roads and urban areas, we created rasters of distance using the tool "Euclidean Distance" in GRASS GIS 7.4. The data of the roads was compiled in National Department of Transport Infrastructure (DNIT, initials in Portuguese language) (http://servicos.dnit.gov.br/vgeo/), available for the year 2016, and the cities information was obtained in Brazilian Institute of Geography and Statistics (IBGE, initials in Portuguese language) (http://mapas.ibge.gov.br/bases-e-referenciais/bases-cartograficas/cartas), available for the year 2015. The raster files were created with GeoTiff extension, resolution of ~ 1 km, with South America Albers Equal Area Conic, Datum SAD69, for limit of Brazil.

After this, we plotted the raster values of model for the rasters distances and raster of land cover, for the limit of Brazil and São Paulo metropolitan region extent, using *raster* and *stats* packages in R, version 3.3.2 (Hijmans 2016, R Core Team 2017). We assessed the relationships between suitability of *E. johnstonei* and land use, distance of roads and distance of urban areas using Generalized Additive Models (GAM), with Binomial error distribution (Zuur et al. 2009). The was used to determine which most plausible variables to explain the suitability of the species (roads, urban areas or land use) we considered the small sample size version of Akaike's Information Criterion (AICc) (Buckland et al. 1993); ΔAICc < 2.0 and wAICc > 0.1 (Burnham and Anderson 2002), including the null model (representing the absence of an effect).

RESULTS

Maxent modeling of 19 training and 6 testing presence records within the native range of *Eleutherodactylus johnstonei* was significant ($p < 0.05$, test AUC = 0.89 ± 0.09).

Temperature Annual Range (20.1 %); Annual Precipitation (18.7 %); Cultivated and Managed Vegetation (16.7 %); and bare soil (11.5 %) contributed to the distribution model considering the native occurrences (Figure 1).

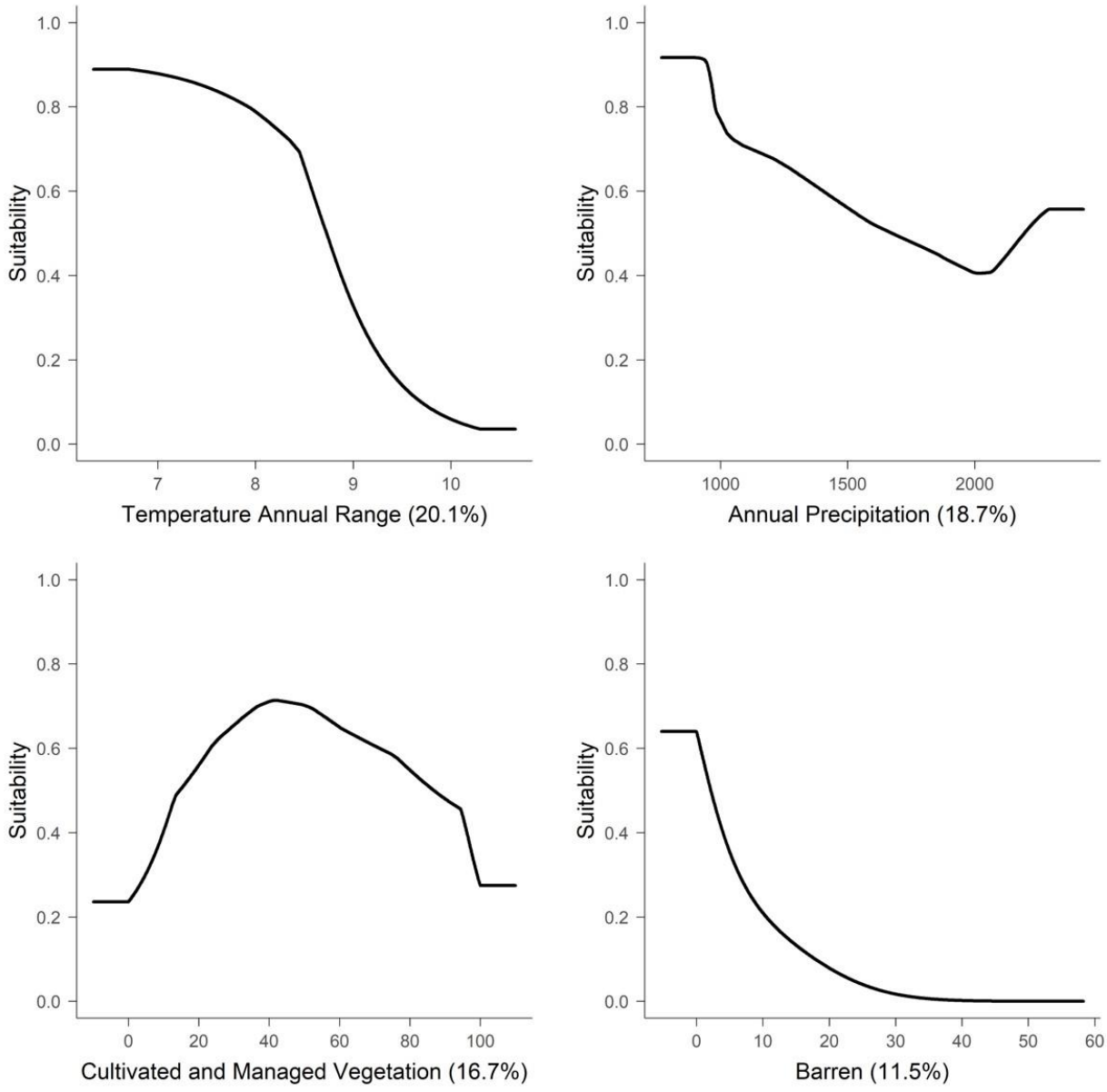

Figure 1. Response curves of the predictor variables that most contribute to model of *Eleutherodactylus johnstonei.*

The projection of the native range distribution model to Brazil showed the most potential occurrence of *Eleutherodactylus johnstonei* in the Southeast, Center-West, and Northeast regions of the country, except for the Northern region where it potentially occurs only in deforested areas of the Amazon forest (Figure 2). The model projection in Brazil showed more expected occurrence in artificial surfaces, grassland, and shrubs (Figure 3).

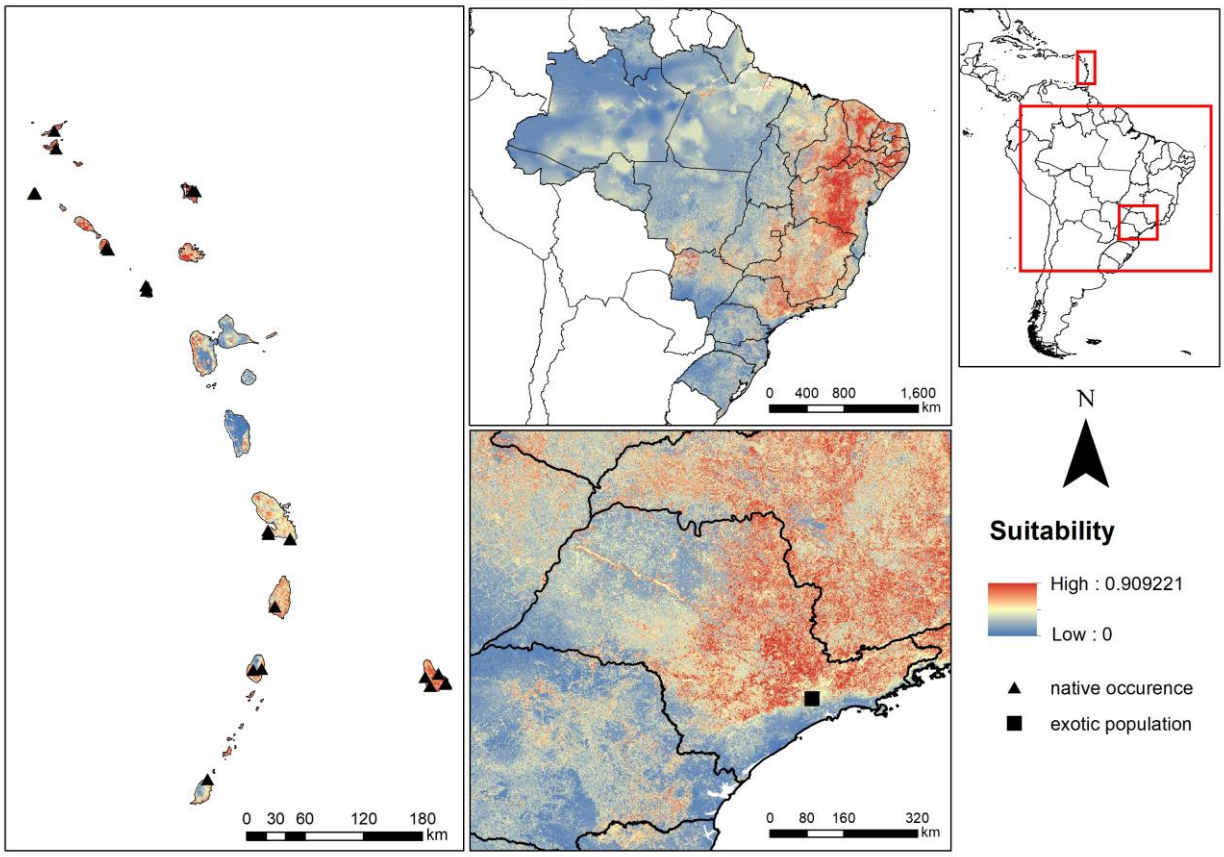

Figure 2. Occurrence points and native MAXENT model of *Eleutherodactylus johnstonei* in Lesser Antilles. Potential of invasion in Brazil and detailed of potential of invasion in the state of São Paulo.

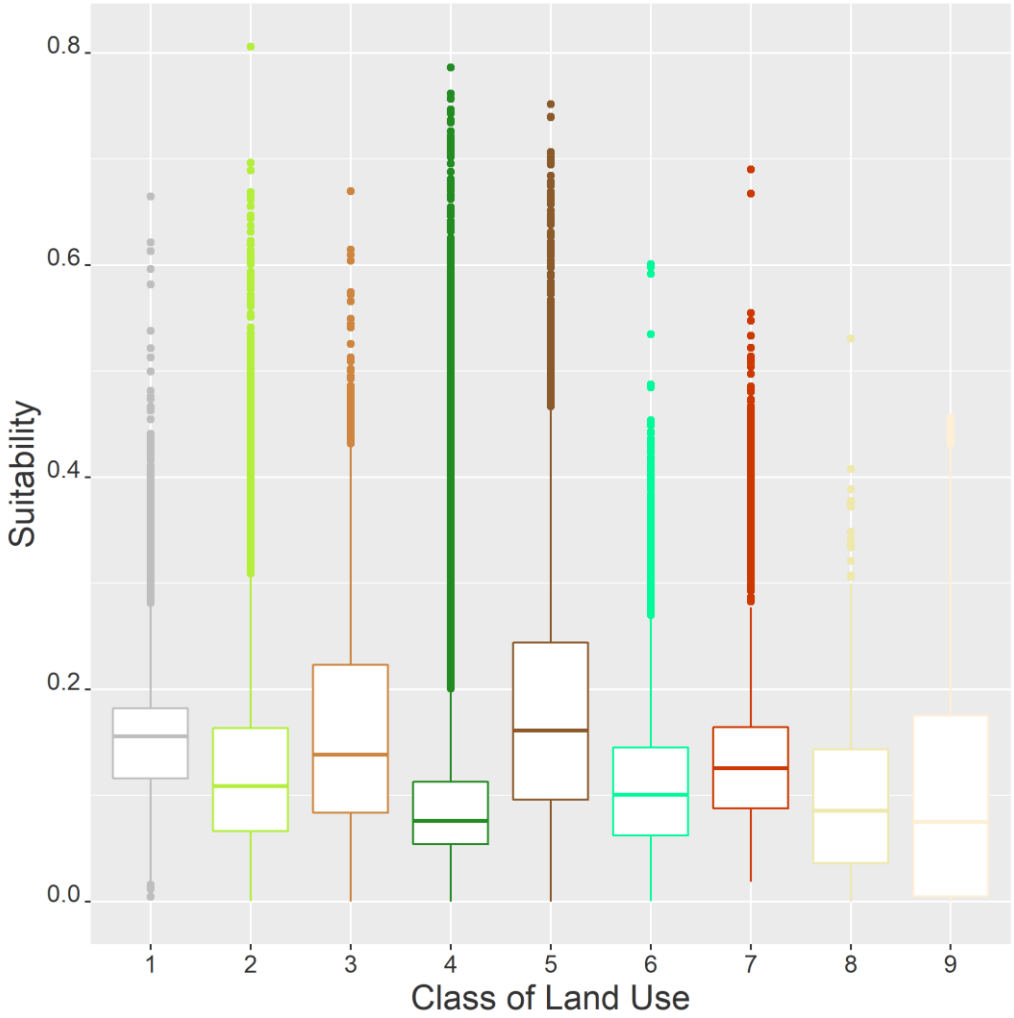

Figure. 3 Suitability of *Eleutherodactylus johnstonei* model and relationship with land use in Brazil. Class of land use: 1) artificial surfaces, 2) crop lands, 3) grasslands, 4) tree-covered areas, 5) shrub-covered areas, 8) herbaceous vegetations, aquatic or regularly flooded, and 9) bare soils.

Suitability for *Eleutherodactylus johnstonei* increases near the cities and roads (Figure 4). However, cities are the landscape attribute that most explain the suitability for this species (Table 2).

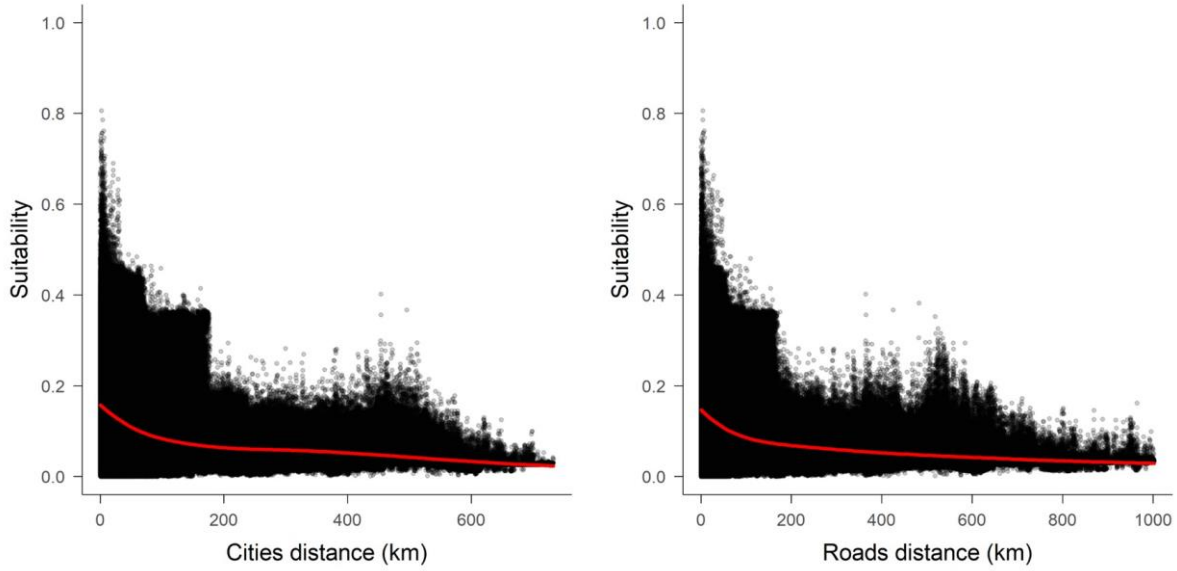

Figure 4. Suitability of *Eleutherodactylus johnstonei* model and relationship with distances of cities (left) and roads (right).

Table 2. Results of Akaike's Information Criterion (AICc) used to determine which attributes (roads, urban areas, and land use) most influence the suitability for *Eleutherodactylus johnstonei*. Land use is the landscape attribute which most influences the suitability for this species.

Attributes	dAICc	Weight
Urban areas	0.00	1
Roads	7,779.03	< 0.001
Land Use	40,179.27	< 0.001
Null model	108,740.173	< 0.001

DISCUSSION

Eleutherodactylus johnstonei is the second non-native invasive amphibian species registered in Brazil (Melo et al. 2014). However, unlike *Lithobates catesbeianus*, which is widely distributed in Brazil, especially in the Atlantic rainforest biodiversity hotspot, *E. johnstonei* has occupied heavily disturbed anthropogenic habitats, being a highly successful colonizer with a high invasiveness potential for South America (Bomford et al. 2009, Rödder 2009).

The recent invasion of *Eleutherodactylus johnstonei* in São Paulo, Brazil, probably will not create a situation similar to that currently observed in *Lithobates catesbeianus*, with populations scattered over natural habitats and pristine protected areas (e.g., Giovanelli et al. 2008, Loyola et al. 2012). Our results confirm the potential for invasion of *E. johnstonei* in anthropic environments, since the variables that express altered habitats were the ones that contributed most to the model. Despite the fact that the invasion of *E. johnstonei* in São Paulo city still appears to be at an early stage and the species is apparently restricted to a small area (Melo et al. 2014), other parts of the São Paulo metropolitan region can be invaded if management and control actions are not taken.

In addition, results showed that the proximities of cities and roads increase the suitability for *Eleutherodactylus johnstonei*. These features can serve as vectors for dispersion of the species in the interior of the country, since most of the roads have some associated habitat in the surroundings, such as artificial surfaces, crop land, and grassland. The state of São Paulo has 50 % of the territory covered by pastures and agriculture, regions that can be of high potential for invasion by this species.

A recent global assessment of alien amphibian impacts made by Measey et al. (2016) showed that *Eleutherodactylus johnstonei* was the only species which has a recorded

economic impact, but lack recorded environmental impact. This result is based on the study of Everard et al. (1990) that showed *E. johnstonei* as a possible vector of leptospirosis. In addition, in Brazil there is a probability that this species will also cause other economic impact; the depreciation in the values of the properties in the neighborhood invaded by this species. The decline in real estate value would be a consequence of the loud vocalizations produced by the chorus of *E. johnstonei* that causes stress and insomnia in the local residents (Melo et al. 2014).

Unlike the American Bullfrog that causes only environmental impacts (Measey et al. 2016), *Eleutherodactylus johnstonei* has the potential to become an invasive exotic species that could bring immeasurable damages to Brazil, especially if its potential to be a vector of leptospirosis is confirmed. The present work is an important subsidy for environmental agencies and decision makers to initiate control, management, and monitoring activities of this species.

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CONCLUSÕES

1. Atualmente, no processo de modelagem da distribuição dos anfíbios, existe um uso massivo de preditores climáticos (temperatura e precipitação).

2. A utilização de variáveis preditoras derivadas de sensores remotos possuem desempenho similar ao das variáveis interpoladas comumente utilizadas.

3. A combinação de varíaveis ecologicamente significantes, derivadas de sensores remotos com variáveis climáticas, resultaram em modelos com áreas mais reduzidas e com um maior detalhamento espacial, sendo menos generalizados quando comparados aos modelos que utilizaram apenas dados climáticos.

4. O uso de variáveis ecologicamente significativas no contexto de empilhamento de modelos foi efetivo para gerar uma riqueza de anfíbios predita similar à efetivamente encontrada no estado de São Paulo.

5. O uso de variáveis derivadas de sensores remotos foi efetivo para modelar o potencial de invasão de *Eleutherodactylus johnstonei* no Brasil. A variação da temperatura anual, precipitação acumulada no ano, cultivos agrícolas e solo exposto foram as variáveis que mais influenciaram a distribuição da espécie. Estas informações podem subsidiar possíveis ações de manejo no local de invasão na cidade de São Paulo, SP.

6. Os dados gerados para o Estado de São Paulo foram apresentados na escala das Unidades de Conservação e dos municípios, faciltando sua utilização como subsídios para futuros planos de conservação de anfíbios. Os dados brutos resultantes da tese serão de livre acesso e estarão disponíveis no endereço eletrônico https://anfibiosnomapa.wordpress.com/.