UNIVERSIDADE VILA VELHA
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA DE ECOSSISTEMAS

MODELOS DE NICHO ECOLÓGICO E A DISTRIBUIÇÃO DE *PHYLLODYTES* (ANURA, HYLIDAE): UMA PERSPECTIVA TEMPORAL DE UM GÊNERO POTENCIALMENTE AMEAÇADO DE EXTINÇÃO POR MUDANÇAS CLIMÁTICAS E INTERAÇÕES BIOLÓGICAS

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SUMÁRIO

RESUMO

MAGESKI, Marcio Marques, D.Sc., Universidade Vila Velha - ES, fevereiro de 2018. **Modelos de nicho ecológico e a distribuição de *Phyllodytes* (Anura, Hylidae): uma perspectiva temporal de um gênero potencialmente ameaçado de extinção por mudanças climáticas e interações biológicas**. Orientador: James Joseph Roper. Co-orientador: Sara Varela.

Usamos modelos de nicho ecológico para avaliarmos os efeitos de mudanças climáticas e interações biológicas sobre a distribuição de *Phyllodytes* sobre tempo. Todas as espécies de *Phyllodytes* usam bromélias obrigatoriamente para reprodução, além de serem endêmicos da Mata Atlântica. Nesse contexto, no primeiro capítulo avaliamos a distribuição atual de *Phyllodytes*, para encontrar os fatores climáticos limitantes e melhoramos esses modelos incluindo riqueza de bromélias. No segundo capítulo, avaliamos a distribuição de *Phyllodytes* e bromélias desde o Plioceno (3 ma), Pleistoceno (21 ka), Holoceno (6 ka) até o presente para tentar determinar o porquê e quando *Phyllodytes* ficou isolado no leste do Brasil. No terceiro capítulo, prevemos como a distribuição de *Phyllodytes* será afetada no futuro (2080-2100) pelas mudanças climáticas, com implicações sobre conservação e áreas protegidas. Nós modelamos a distribuição de *Phyllodytes* usando Sistema de Informação Geográfica (SIG) e métodos de máxima entropia (MaxEnt), com 75% de dados para treino e 25% para teste, com 1000 iterações e 2 multiplicador beta. Em todos os modelos usamos a extensão da América do Sul como paisagem. Os modelos do primeiro capítulo mostraram uma melhoras nas acurácias das predições e no valor de AICc quando as bromélias foram incluídas. O modelo clima + bromélias mostra que a distribuição potencial atual de *Phyllodytes* ficou mais restrita à região costeira em relação aos demais, embora em uma região considerada hotspot de bromélias. Assim, a distribuição de bromélias, além de clima, é limitante para *Phyllodytes*. Os modelos do segundo capítulo mostraram que a distribuição potencial de *Phyllodytes* aumentou desde o último máximo glacial. Além disso, os modelos mostraram que a distribuição dos sapos poderia ter sido ainda maior com limites unilaterais. Nessas regiões sempre havia clima favorável e bromélias disponíveis, o que implica que nunca foram limitante no passado. Sobretudo, *Phyllodytes* parece evitar a sobreposição com outros sapos potencialmente predadores e competidores. Isso sugere que por conta de competição e predação *Phyllodytes* foi forçada a ocupar áreas menos favoráveis climaticamente. Os modelos do terceiro capítulo mostraram uma redução considerável da distribuição de *Phyllodytes* no futuro, principalmente no cenário mais pessimista de aumento de temperatura. Nesse contexto, a distribuição de *Phyllodytes* é predita somente para os estados do Espírito Santo e Rio de Janeiro e ainda com uma viabilidade climática reduzida. Isso mostra a urgente necessidade de implantar novas unidades de conservação, considerando a dinamicidade climática, de modo à assegurar a conservação do gênero.

PALAVRAS-CHAVE: Mata Atlântica, anfíbios, mudanças climáticas, bromélias, MaxEnt.

ABSTRACT

MAGESKI, Marcio Marques, D.Sc., Universidade Vila Velha - ES, february 2018. **Ecological niche models and the distribution of *Phyllodytes* (Anura, Hylidae): a temporal perspective of a genus potentially threatened by extinction by climate changes and biological interactions.** Advisor: James Joseph Roper. Co-advisor: Sara Varela.

We used ecological niche models to evaluate the effects of climate change and biological interaction on *Phyllodytes* distribution over time. All species of *Phyllodytes* use bromeliads obligatorily for reproduction and are endemic to the Atlantic Forest. In this way, on the fist chapter we evaluated the current distribution of the genus to found climatic limiting factors and to improve this models including a bromeliad richness. On the second chapter, we evaluated the distribution of *Phyllodytes* and their bromeliad since Pliocene (3 ma), Pleistocene (21 ka), Holocene (6 ka) to present to attempt to determine why and when *Phyllodytes* became isolated in eastern Brazil. On the third chapter, we predicted how Phyllodytes distribution will be affected by future climate changes, with implications about conservation and protected areas for conservation. We modelled the distribution of *Phyllodytes* using Geographical Information System (GIS) and maximum entropy methods (MaxEnt) and, with 75% of the data for training and 25% for testing, with 1000 iterations and 2 beta multiplier. All models used the extent of South America as landscape. On the first chapter, the models showed that inclusion of bromeliads improved the climatic models and AICc. Also, the models climate + bromeliads showed that distributed of Phyllodytes was more closed to the coast than other models, in a region considered as a hotspot of bromeliad. Thus, the distribution of bromeliads is limiting for *Phyllodytes*, besides climate. The models of the second chapter showed that Phyllodytes distribution increased since the last glacial maximum and that those distribution could have been more widespread with unilateral limits. In those predicted range ever had suitable climate and bromeliads, which implies that were not limiting in the past. However, *Phyllodytes* apparently avoid overlap with distribution of other bromeliad frogs. This suggest that, probably, because competition and predation *Phyllodytes* was forced to the regions less favourable climatically. The models of third chapter showed that distribution of Phyllodytes will decrease in the future, mainly in pessimistic scenario of increasing temperature. In this way, Phyllodytes distribution was predicted only for the Espírito Santo and Rio de Janeiro States, with low climatic suitability. This suggest the urgent needs to implement new protected areas, considering climatic dynamics, to conservation of the genus.

KEY WORDS: Atlantic Forest, amphibians, climate change, bromeliads, MaxEnt.

INTRODUÇÃO GERAL

O clima global variou nos últimos 3 milhões de anos, alternando entre períodos quentes-úmidos e frios-secos (Barnosky 2008, Boer et al. 2014). Essas variações inflenciaram a fenologia, interações biológicas e, principalmente a distribuição geográfica das espécies (Root et al. 2003, Araújo et al. 2004, Parmesan 2006, Williams et al. 2007, Raxworthy et al. 2008, Lemes e Loyola 2013). Nesse contexto, estudos têm se preocupado em analisar os efeitos de mudanças climáticas globais na distribuição de espécies sobre o tempo para compreender padrões biogeográficos evolutivos e atuais, bem como gerar previsões futuras frente a diferentes cenários conservacionistas (Pie *et al.* 2013; IPCC 2014; Duan *et al.* 2016; Leite *et al.* 2016; Pimiento *et al.* 2016).

As espécies respondem às mudanças climáticas de formas variadas, podendo dispersar, adaptar ou serem extintas (Berg *et al.* 2010). Essas respostas irão depender da tolerância de cada espécie às variações, podendo aumentar ou retrair a distribuição. Por exemplo, foi predito que a distribuição potencial da abelha *Euglossa marianae* aumentou no norte da América do Sul desde o último máximo glacial (21 ka) e contuará aumentando no futuro por consequência das mudanças climáticas (Nemésio *et al.* 2016). Por outro lado, as plantas europeias *Carex bigelowii*, *Blechnum spicant* e *Taxus baccata* tendem a reduzir as distribuições atuais, principalmente em latitudes intermediárias, devido ao aumento da temperatura no futuro (Pearson e Dawson 2003). Compreender esses padrões, e como variam em função do tempo, é imprescindível para desenvolver estratégias eficazes de conservação frente à esse preocupante panorama global no qual muitas populações já estão ameaçadas ou localmente extintas.

Anfíbios são extremamente sensíveis às variações climáticas como consequencia de baixa capacidade de dispersão, respiração e reprodução (Duellman e Trueb 1994; Foden et al. 2008; Ochoa-Ochoa et al. 2012).Por isso, esses animais são modelos perfeitos para avaliação dos efeitos de mudanças climáticas sobre a distribuição geográfica da biodiversidade. Aproximadamente, um terço de todas espécies de anfíbios estão ameaçadas e 52% são sensíveis às mudanças climáticas, fazendo desse táxon um dos mais ameaçados globalmente (Stuart *et al.* 2004; Foden *et al.* 2008; Hof *et al.* 2011). As consequências das mudanças climáticas para anfíbios são variadas. Por exemplo, são previstas mudanças nos padrões de diversidade de anfíbios, com perdas de até 20% das distribuições originais para a China (Duan et al. 2016). Na América do Sul, são preditas contrações da distribuição potencial de algumas espécies de *Dendropsophus* da região central para o sudeste do Brazil (Vasconcelos e Nascimento 2015). Ao passo que, são previstos aumentos de distribuição para a espécie invasora de Rã Touro *Lithobates catesbeianus* na Mata Atlântica (Loyola *et al.* 2014).

Além de clima, as interações biológicas também influenciam a distribuição geográfica das espécies (Davis et al., 1998, Araújo e Luoto 2007, Lentz et al., 2008, Gutiérrez et al. 2014) facilitando ou inibindo a dispersão (Silvertown 2004, Bascompte 2009, Van Dam 2009, Jankowski et al. 2013). Aparentemente, alguns anuros tiveram vantagens ao usar a água armazenada em bromélias como refúgio, durante clima mais seco (Teixeira et al. 1997, Schneider e Teixeira, 2001, Mageski et al. 2016). Isso é possível uma vez que ao acumularem água por longos intervalos de tempo, as bromélias formam um microambiente adequado para uso (Schiesari *et al.* 2003; Mageski *et al.*, 2016). Assim, alguns anfíbios evoluiram em direção à associações obrigatórias com bromélias e por isso, atualmente, dependem exclusivamente dessas plantas durante o ciclo de vida (Peixoto 1995). Essa dependencia, lhes permitem habitar em ambientes onde a água é limitante, os quais provavelmente seriam inóspitos para outras espécies (Peixoto 1995). Por outro lado, esses anfíbios somente poderão habitar áreas com bromélias, o que poderá limitar a distribuição para áreas mais adequadas climaticamente. Assim, no caso de anfíbios que usam bromélias obrigatoriamente, a distribuição das bromélias juntamente com o variações climáticas, provavelmente influenciaram a distribuição das espécies ao longo do tempo.

O gênero *Phyllodytes* (Wagler, 1830) compreende 17 espécies (13 descritas e 4 em descrição) endêmicas da Mata Atlântica, leste do Brasil (Frost 2017). Todas as espécies desse gênero usam bromélias obrigatoriamente para reprodução (Haddad et al. 2013). Atualmente, *Phyllodytes* é encontrado usando 19 espécies de bromélias dos gêneros *Vriesea, Aechmea*, *Neoregelia*, *Alcantarea*, *Encholirium*, *Hohenbergia* e *Quesnelia*, as quais também são usadas por outras espécies de anfíbios (Sabagh et al. 2017).

Com estas considerações, aqui propõe-se examinar a complexa relação entre clima, bromélias e anuros, na distribuição temporal do gênero *Phyllodytes*. Usando algoritmo de máxima entropia (MaxEnt) e Sistemas de Informação Geográfica (SIG), desenvolvemos modelos para 1) entender a distribuição atual e identificar os fatores limitantes, 2) compreender o histórico-evolutivo das espécies e as consequências na distribuição atual e 3) prever como mudanças climáticas futuras irão influenciar a distribuição das espécies. Assim, a presente tese de doutorado está dividida em três capítulos, seguindo uma sequência lógica. No primeiro capítulo, examinamos a distribuição atual do gênero *Phyllodytes* para explicar o porque está limitado na Mata Atlântica do leste do Brasil. No segundo capítulo, buscamos entender o contexto histórico-evolutivo, examinando a distribuição prevista para *Phyllodytes* desde o Plioceno (3 ma), passando pelo Pleistoceno (21 ka, Último Máximo Glácial), Holoceno (6 ka) até o presente, considerando as limitações impostas por interações com bromélias e outros anuros. E, no terceiro capítulo prevemos como será a distribuição de *Phyllodytes* diante de diversos cenários conservacionistas para o intervalo de 2080-2100, com implicações sobre áreas protegidas e como estarão no futuro.

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Austral Ecology

CAPÍTULO 1

Niche modeling indicates that the Brazilian heart-tongued frogs (*Phyllodytes* spp.) are probably endangered

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Abstract Poorly known species may be cryptically endangered, especially when they inhabit fragmented and threatened habitats. Heart-tongued frogs (genus *Phyllodytes*, family Hylidae, Lophyohylinae) comprise 17 species of poorly known frogs that have obligatory associations with tank bromeliads. The distributions of all species are restricted to a small, extremely fragmented, region of Atlantic Forest in eastern Brazil. We model climate and tank bromeliad distributions to better understand frog distribution limits. Using records from several sources for frogs and bromeliads with climate data from WorldClim, we modeled the distribution of *Phyllodytes* using maximum entropy. We compared climate and altitude within the distribution and nearby to test how climate may limit distribution. Climate together with bromeliad distributions provided the best model and predicted the smallest suitable area for *Phyllodytes* that was larger than that occupied, from the state of Paraíba in the north to Rio Grande do Sul in the south. *Phyllodytes* occurs in lower elevations that are warmer, wetter and less variable than the surrounding regions where it does not occur, and dispersal is apparently limited by the surrounding, inhospitable, region. Dispersal limitation and habitat fragmentation have relegated *Phyllodytes* to many very small habitat fragments. With many species in this genus being known from a single or few samples, this unfortunate combination of limitation and fragmentation suggests that some or all species of *Phyllodytes* may be threatened with extinction, especially if habitat fragmentation continues at its present pace in eastern Brazil.

Keywords: Amphibians, bromeliads, forest fragmentation, Maxent, endemism, endangered species.

INTRODUCTION

A species may be endangered due to habitat fragmentation and limited distribution, but due to limited biological information, this possibility is unrecognized. In eastern Brazil, only a small fraction of the original Atlantic Forest remains (~8%), and what remains is severely fragmented (Ribeiro *et al.* 2009, Tabarelli *et al.* 2010, SOS Mata Atlântica 2014). In this forest, most (90%) species of amphibians are endemic (Bornschein *et al.* 2016a) and due to habitat requirements and dispersal limitation, fragmentation and loss of habitat may be driving several species towards extinction (Haddad *et al.* 2013).

The heart-tongued frogs (genus *Phyllodytes*, family Hylidae) comprises 17 species (13 described and four under description) that are all endemic in the Atlantic Forest of eastern Brazil (Fig. 1A). All *Phyllodytes* (Wagler 1830) are obligate users of tank bromeliads (in which water accumulates and remains for long time intervals). Bromeliad – frog associations are common, poorly understood and potentially very important for conservation (Sabagh et al. 2017). Bromeliads are both habitat and breeding sites and so bromeliads with forms that perennially retain water are those that are used (Schiesari *et al.* 2003; Mageski *et al.* 2016). *Phyllodytes* has been found in 19 species of bromeliads, some of which are widespread in the Atlantic forest of eastern Brazil (Fig. 1B, Appendix S1). The use of water storage in bromeliads is important in sandy coastal plains and lowland forests, in which *Phyllodytes* occur (Fig. 2A, 2B), because high temperature (Fig. 2C) and water limitations, given the sandy soil and slope of the terrain, respectively, besides annual precipitation is high (Fig. 2D).

The genus *Phyllodytes* arose in the Tertiary (ca. 35.4 mya, Duellman *et al.* 2016) and today is restricted to a small region of the Atlantic Forest (Fig. 1A), yet the subfamily Lophyohylinae is widespread in South and Central America, some Caribbean islands and southern North America (Frost 2017, IUCN 2017, Appendix S2). *Phyllodytes* and *Phytotriades* (the two oldest genera, the latter of which is now restricted to the eastern Venezuela and island of Trinidad) are unique genera among the

Lophyohylinae because they are obligate-associates with bromeliads (Bokermann 1966; Haddad & Prado 2005; Jowers *et al.* 2008, Rivas *et al.* 2015, Duellman *et al.* 2016). At the time of the origin of *Phyllodytes*, the Amazon and Atlantic Forests were (and several times since) a single continuous forest in which it is likely that *Phyllodytes* ancestral dispersed to the Atlantic Forest (Bigarella *et al.* 1975; Duellman *et al.* 2016). As the forests separated in the Tertiary (Bigarella *et al.* 1975) *Phyllodytes* apparently became extinct everywhere except for its current range (Fouquet *et al.* 2012a; 2012b; Bornschein *et al.* 2016a; 2016b).

Because of the very limited distribution of all species in the genus (especially those with a single record), their dependence on bromeliads, and due to the extremely fragmented nature of the original habitats in eastern Brazil, we predict that many or perhaps all of these species should be considered to be endangered. Here, to lend support to that idea, we examine the current distribution of the genus *Phyllodytes* to explain why it is limited to the Atlantic Forest of eastern Brazil and to examine the consequences of that limitation in the current context of habitat fragmentation. Our objectives are: 1) to map the current distribution of the genus *Phyllodytes,* 2) to map the distributions of the species of bromeliads in which *Phyllodytes* has been found, 3) in concert with the distributions of frogs and bromeliads, examine potential climatic and biotic factors that may limit, or have limited, the distribution of *Phyllodytes*. Finally, we place this information in the context of current understanding of the genus and its species to suggest that they are endangered.

MATERIALS AND METHODS

Data sources

Frog species

Occurrences of the 12 genera in the Lophyohylinae were obtained by searching online zoological databases in Brazil, Germany, France, Spain and the United States, using Species Link (CRIA 2016), Global Biodiversity Information Facility (GBIF 2016) and relevant literature. For the genus *Phyllodytes* we also included field observations from 2007 to 2015 in the state of Espírito Santo, Brazil. In the field, vocalizing frogs were located by their calls and additional frogs were found by searching in the appropriate tank bromeliads (Rödel & Ernst 2003; Mageski *et al.* 2015). Data gathered from museums, publications and the field included date, latitude, longitude, altitude (we used GPS Map GARMIN® 60csx) and the species of bromeliad in which the frog was found (when available in the literature and museum records, and always in our field samples). We used ArcMap 10 (ESRI 2011; Kozak *et al.* 2008) to map the distribution of the genus (Fig. 1A). To place the genus *Phyllodytes* in a biogeographical context, we use ArcMap 10 to plot the coordinate points and mapped the distributions of the 12 genera in the subfamily Lophyohylinae (Faivovich *et al.* 2005; Jowers *et al.* 2008; Wiens *et al.* 2010; Frost 2017; Duellman *et al.* 2016).

Phyllodytes and *Phytotriades* are the oldest genera in the subfamily in which all species are the only genera in the subfamily obligatorily associated with bromeliads, and both have the most restricted and isolated distributions (Bokermann 1966; Haddad & Prado 2005; Jowers *et al.* 2008, Rivas *et al.* 2015, Duellman *et al.* 2016, Appendix S2). *Phyllodytes luteolus* is the most common, with the largest distribution, of the 17 species in the genus and is a typical representative. These small frogs have an average snout-vent length of 21.0 mm and weigh 0.74 g (Mageski *et al.* 2015). These small frogs apparently tend to remain within a bromeliad clump and so their ability to disperse depends on the distance between bromeliads. The ecology of the other species is essentially unstudied, and we assume that all species in the genus are similar in ecology to *P. luteolus*.

Bromeliads used by the frogs

Summing reports and our records, frogs were found in a total of 19 species of bromeliads (Table 1). We searched for (georeferenced) records of these 19 species in Species Link, Tropicos (2016), and the

Smithsonian Botany collection (2016). With those coordinates, we mapped the distribution of those 19 species. Because we had no reason to think that *Phyllodytes* preferred any bromeliad species, we simplified the map to show the distribution of each species (number of species per pixel) without identifying the species so that the map indicates the presence of one or more species (Fig. 1B). We also noted which species of bromeliads had ranges outside the area of interest, and where, as potentially important for understanding the distribution of *Phyllodytes*. We did not assume that *Phyllodytes* are restricted to these bromeliads and recognize that they may use many more (Sabagh et al. 2017), but rather we preferred to use the available information as a conservative estimate.

Climate

We obtained altitude and bioclimatic data from WorldClim (Hijmans *et al.* 2005) with a resolution of 30 arc-seconds (~1km). We chose variables that we biologically meaningful to the frogs and kept only those variables that were uncorrelated or relatively weakly correlated ($r < 0.70$) to avoid collinearity. Climate variables include isothermality (bio 3), maximum temperature of the warmest month (bio 5), minimum temperature of coldest month (bio 6), annual range in temperature (bio 7), annual precipitation (bio 12), seasonality of precipitation (bio 15) and precipitation of the driest quarter (bio 17). We rasterized these using the package raster (Hijmans *et al.*, 2016a) in R 3.3.0 (R Core Team 2016).

Analysis

Ecological Niche Modeling (ENM)

We modeled the distribution of *Phyllodytes* using presences and climate using maximum entropy methods (MaxEnt) in the dismo package (Phillips *et al.* 2006; Hijmans *et al.* 2016b), with 75% of the data for training and 25% for testing, with 1000 iterations and 2 beta multiplier. All models used the extent of South America (-30º to -90º longitude, -60º to 15º latitude) as landscape and we modeled the distribution of *Phyllodytes* in three ways, using 1) climate, 2) bromeliad distributions (as described above) and 3) climate combined with bromeliad distributions. We evaluated the models using Area Under the Receiver Operating Characteristics (ROC) Curve (AUC) and True Skill Statistic (TSS, Allouche *et al.* 2006; Elith *et al.* 2010; Clements *et al.* 2012; Zank *et al.* 2014; Nemésio *et al.* 2016). In addition to AUC and TSS, we compared the corrected Akaike Information Criterion (AICc, Hurvich & Tsai 1989) in the ENMeval package (Muscarella *et al.* 2016) among the resultant three models to determine which best explained the frog distribution. We also calculated the range area (km^2) predicted, using the raster package in R.

Comparison of climate

To test whether *Phyllodytes* is now isolated due to climate, we compared climate where *Phyllodytes* occurred with adjacent areas where it has never been recorded. To do so, we created two imaginary bands similar in format and parallel to the area in which the frog is present (thereby forming three parallel bands) and we used the climate data within those bands for comparison. We label the bands as within the range, adjacent to the range and west of the range. We used climate values at the points where *Phyllodytes* was found and the same number of points chosen randomly in the other two bands. We also chose, within the range of *Phyllodytes*, the same number of random points, but at which the frog had not been reported. Thus, we had four treatments for comparing climate (range and present, range and absent, adjacent to the range, west of the range) to test the prediction that climate may limit the frog distribution. We compared the four treatments using altitude and three climate variables using Analysis of Variance (ANOVA).

RESULTS

We gathered 50 independent coordinates for locations of *Phyllodytes* from museums without reference to the bromeliad in which the frog was found. We added 26 geographic locations comprising 949 records of frogs in 19 species of bromeliads from our fieldwork and other studies (Appendix S1). Thus, we used 76 independent coordinates of frog locations in modeling (Fig. 1A). Due to the scale of the climate data, more than one record of frog was often found within the same limits (30 arc seconds) and thus the number of frog records is much greater than the number of geographic locations.

We gathered 1,525 independent coordinates of the species of Lophyohylinae locations from museums, our fieldwork and published studies. This mostly tropical subfamily includes 12 genera and 84 species distributed from southern Florida in the southern United States to northern Argentina, from the Atlantic to the Pacific coasts in northern South America, and in the Caribbean (Appendix S2).

Ecological niche modeling of climate resulted in AUC = 0.99 (in both, in training and testing), TSS = 0.97 and a predicted area of ca. 844,183 km^2 to be climatically adequate for *Phyllodytes*, from Paraíba to Rio Grande do Sul (Fig. 3A, C). The three most important variables (as measured by permutation importance, PI) in this model were annual range in temperature (PI = 34.2), isothermality (30.1) and precipitation of the driest quarter (17.2). This model generated an AICc of 1925.7.

Second, modeling the 19 bromeliad species (as the likelihood of finding 0 – 9 species in an area) to predict the distribution of the frog species, AUC for training and testing were 0.99, TSS = 0.97 and AICc was 2074.5. This model predicted an area of ca. 1,200,000 km^2 as adequate for *Phyllodytes* and was exactly the same distribution as that of the probability of finding 0 – 9 bromeliad species (Fig. 1B).

Climate together with bromeliads resulted in AUC = 0.99 (in both, in training and testing) and TSS = 0.98. This model had the lowest AICc (1889.4, ΔAICc = 36 compared to the next model). This model also predicted the smallest area adequate for *Phyllodytes*, ca. 251,714 km^2 from Paraíba to Rio Grande do Sul (Fig. 3B, D). In this model, the three most important variables were annual range in temperature (PI = 60.6), bromeliads (PI = 18.5) and precipitation during the driest quarter (PI = 11.7).

In comparing altitude and climate between the three bands and where *Phyllodytes* occurs, the two adjacent bands were very different from the region where the frog is found. The random points within the region where *Phyllodytes* was found, but where frogs were never reported, were similar to those where the frogs were found (Fig. 4). Altitude tended to be much higher in the adjacent band and farther west ($F_{3, 299} = 35.1$, $r^2 = 0.26$, $P < 0.001$, Fig. 4A). Isothermality was lowest where *Phyllodytes* is found ($F_{3, 300} = 14.4$, $r^2 = 0.13$, $P < 0.001$, Fig. 4B). Annual range in temperature was lower within the distribution of *Phyllodytes* ($F_{3, 299} = 44.6$, $r^2 = 0.31$, $P < 0.001$, Fig. 4C). Finally, rainfall during the driest quarter was much greater within the *Phyllodytes* distribution ($F_{3, 299} = 64.9$, $r^2 = 0.39$, $P < 0.001$, Fig. 4D). Thus, with these four variables, we demonstrate that the region adjacent to the distribution of *Phyllodytes* is very different from that within the region in which the genus is found. Specifically, temperature is less variable and the driest time of year is wetter and bromeliads are present, where the frogs are found. Thus, *Phyllodytes* tend to be found in lowland rain forest (< 1000 m), where temperature range from 24.0 – 25.9º C and annual precipitation from 1,309 – 2,119 mm (Fig. 2A, 2B, 2C, 2D), and these areas tend to be found in the sandy coastal plains (locally called *restinga* forests).

DISCUSSION

Phyllodytes species are all currently restricted to the Atlantic Forest where appropriate bromeliads are found, and where temperatures are less variable and dry seasons are somewhat wetter than nearby in the Atlantic Forest remnants. Although all *Phyllodytes* spp. are currently limited to the region between Paraíba in the north and Espírito Santo in the south, our models suggested that areas with suitable climate extended to the southern limits of the Atlantic Forest (Rio Grande do Sul). Climate modeling indicates that the combination of available bromeliads and climate restricts these frogs to this region and, due to dispersal limitation, they cannot reach new habitats because they would have to cross inhospitable areas. The area determined to be climatically appropriate for frogs tends to be lowland, warmer, wetter and less variable than the surrounding regions. These differences are important as mechanisms that may limit dispersal of *Phyllodytes* and thereby explain frog isolation in a limited subset of the region that is climatically suitability in the coastal Atlantic Forest. *Phyllodytes* is not unique in isolation and endemism, and other species of frogs of the Atlantic Forest are also isolated and endemic, often in habitat fragments found at higher elevations (Bornschein *et al.* 2016a; 2016b).

The information we gathered on bromeliads demonstrates that *Phyllodytes* use only a small subset (19 species) of the more than 430 species of tank bromeliads available in the Brazilian Atlantic Forest (Martinelli *et al.* 2008, Sabagh *et al.* 2017). Also, frogs are more likely to be found in some than others. Today, *Phyllodytes* was found in two of 166 species of *Vriesea,* 11 of 136 species of *Aechmea*, one of 97 *Neoregelia*, one of 16 *Alcantarea*, one of three *Encholirium*, two of 24 *Hohenbergia* and one of 16 *Quesnelia*. While we cannot know the availability of all of those species, these tendencies suggest that *Phyllodytes* are selective of some aspect (such as perenniality) that is only readily available in some species of bromeliads. Thus, bromeliad availability will limit the occurrence of *Phyllodytes*. Bromeliad choice may be common, and *P. luteolus* was found to occur more often in smaller plants with a disproportionately larger number of leaves (Mageski *et al.* 2016). *Phyllodytes melanomystax* tended to be found in bromeliads that were within a greater local density of other bromeliads and frogs seemed to avoid plants in which the water had more debris (Cunha & Napoli 2016). Thus, in addition to climate, a complex interaction between bromeliad morphology, local bromeliad abundance and characteristics of water contained in the bromeliad may be important determinants of tank use by the frogs. Also, because the distributions of some species of bromeliads used by the frogs are larger than that of the frogs (Fig. 1B), the complex interaction between climate and bromeliads seems to limit frog distributions.

Today, all records of *Phyllodytes* are within a relatively narrow corridor between the highlands and the coast. Nine of these species are known from one to three records, and multiple records of species are all within small geographic areas (Fig. 5). Since the colonization of Brazil, this coastal plain has been repeatedly deforested, fragmented and used for intensive agriculture (Colombo & Joly 2010). During intervals when fragmented, both frogs and bromeliads would have been isolated in areas not suitable for agriculture. When and if the landscape recovered (during intervals with less intense agriculture), bromeliads, which are wind or bird dispersed, may have rapidly recolonized newly available areas (Gomes *et al.* 2008; Cascante-Marín *et al.* 2009). Obligate bromeliad frogs, on the other hand, must disperse from bromeliad clump to bromeliad clump. The current state of habitat fragmentation in this region is dire, with only a small fraction of original habitat remaining (~8%, SOS Mata Atlântica 2014, Fig. 5). Thus, without corridors connecting the many fragments, each fragment of habitat may become an island within an inhospitable matrix for *Phyllodytes*, with all the consequences implied by isolation (Lomolino *et al.* 1995; Marsh *et al.* 1999; Parra-Olea *et al.* 2012; Calkins *et al.* 2012; Ferreira *et al.* 2016; Grossen *et al.* 2016).

Our model including climate together with bromeliad distributions provided the best fit (by ΔAICc) and predicted a suitable distribution for *Phyllodytes* that was more restricted to coastal areas than the climate-only model. Surprisingly, this predicted area for *Phyllodytes* is also a region of a diversity hotspot for bromeliads (Smith 1955; Martinelli *et al.* 2008), which seems to support the obligatory bromeliad connection. Only two genera in the Lophyohylinae have all species obligatorily associated with bromeliads, *Phyllodytes* and the monotypic *Phytotriades*, which are also the two oldest genera (Haddad & Prado 2005; IUCN 2017; Frost 2017; Duellman *et al.* 2016). *Phytotriades auratus* is restricted to the eastern Venezuela and island of Trinidad, and have only been found breeding in the epiphytic giant tank bromeliad *Glomeropitcairnia erectiflora* (Jowers *et al.* 2008; Rivas & Freitas 2015). Interestingly, both of the obligate bromeliad users *Phyllodytes* and *Phytotriades* have restricted distributions relative to the other genera in Lophyohylinae (Appendix S2). Thus, apparently a consequence of obligatory bromeliad use is limited distribution, perhaps through dispersal limitation.

Currently and historically, extensive and ongoing habitat loss in the Atlantic Forest has resulted in only a small and fragmented fraction remaining (~8% of the original Atlantic Forest remains, SOS Mata Atlântica Institute 2014). Thus, due to human impact all populations of all species of *Phyllodytes* are now facing habitat fragmentation into many, probably genetically isolated, populations. Thus, based on the combination of 1) narrow, favorable climatic conditions and consequently small real and potential distributions, 2) extremely small apparent distributions of some species of *Phyllodytes* (most known from fewer than 10 records), 3) their obligatory association with bromeliads, and 5) their highly fragmented habitat, we suggest that all or most *Phyllodytes* species are likely to be endangered with extinction. Our models and data bring us to the conclusion that the current conservation status of this frog genus should be reconsidered. We urge that these species quickly be studied to determine the extent of their individual distributions and their associations with bromeliads to ensure that protective measures be taken before they go extinct unnoticed.

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Table 1. The 19 species of Bromeliaceae in which *Phyllodytes* was found when noted, with the number of records that provided geographic coordinates for modeling (column Records). The column N (species) indicates the number of observations of each species of frog in that bromeliad. *Phyllodytes acuminatus* (P. a), *P. brevirostris* (P. b), *P. edelmoi* (P. e), *P. kautskyi* (P. k), *P. luteolus* (P. l) and *P. melanomystax* (P. m).

Bromeliad	Records	N (species)
Aechmea aquilega	97	1 (P. m)
A. blanchetiana	24	2 (P. k, P. l)
A. chlorophyla	26	1 (P. k)
A. lamarchei	47	1 (P. l)
A. leptantha	58	1 (P. a)
A. lingulata	128	1 (P. e)
A. nudicaulis	596	2 (P. k, P. l)
A. patentissima	60	1 (P. b)
A. phanerophlebia	68	1 (P. k)
A. saxicola	45	1 (P. l)
A. victoriana	38	1 (P. l)
Alcantarea extensa	23	1 (P. l)
Encholirium spectabile	144	1 (P. a)
Hohenbergia augusta	52	1 (P. l)
H. littoralis	36	1 (P. m)
Neoregelia cruenta	18	1 (P. l)
Quesnelia quesneliana	38	1 (P. l)

Peixoto & Cruz 1988; Caramaschi *et al.* 1992; Teixeira *et al.* 1997; Eterovick 1999; Papp & Papp 2000; Schineider & Teixeira 2001; Juncá & Borges 2002; Peixoto *et al.* 2003; Simon & Gasparini 2003; Caramaschi & Peixoto 2004a; Caramaschi *et al.* 2004b; Peixoto & Pimenta 2004; Juncá 2006; Caldas et al. 2011; Ferreira *et al.* 2012; Simon & Peres 2012; Campos *et al.* 2014; Mageski *et al.* 2014; Magalhães *et al*. 2015; Mageski *et al.* 2015; 2016; Cunha & Napoli 2016; Motta-Tavares *et al.* 2016; Ruano-Fajardo *et al.* 2016; Frost 2017; present study.

Figure legends

Figure 1. Context of the geographic distribution of the genus *Phyllodytes* in eastern Brazil and the location of this distribution in South America. A. Points indicate the locations in which *Phyllodytes* have been found. B. The distribution of the 19 bromeliads used by *Phyllodytes*. As these species seemed to be used without bias (awaiting further study), the map indicates the number of species found and so varies from 0 (white) to 9 (darkest grey) were the distributions of the most species overlap. ES, Espírito Santo.

Figure 2. Map detailing the context of this study. A. Plant formations in eastern Brazil, illustrating separation of the Atlantic Forest from the Amazon Forest due to the intervening Caatinga and Cerrado (savanna habitats, the former drier than the latter), DOR indicates the Doce River and SFR the São Francisco River. B. Elevation, showing the coastal mountain. C. Average annual temperature, showing the hotter environment to the north and west, and colder to the south. D. Annual precipitation (mm).

Figure 3. Modeled suitability for *Phyllodytes*. A - The modeled distribution of suitable areas based on climate. B - Modeled distribution of suitable areas based on climate and the 19 bromeliads. We do not show the modeled distribution based on bromeliads alone, as that model is identical to Figure 1B. C and D indicate the binary predictions of suitable habitat referred to in A and B respectively. For acronyms of Brazilian states see Appendix S1.

Figure 4. Comparisons of (A) altitude, (B) isothermality, (C) annual range in temperature and (D) precipitation during the driest quarter between the points at which *Phyllodytes* was found (Present), random points within that area but where the frog was not found (Absent), a band of similar area adjacent to and west of the observed distribution (Adjacent) and another band farther west, next to the former band (West). Figures show the mean values with their 95% confidence intervals. The inset map shows the region in Brazil and the three bands used to compare with the region in which *Phyllodytes* is found. Black indicates where *Phyllodytes* was Present, and where random points where *Phyllodytes*

was not found (Absent) were used. Dark grey is the Adjacent, and light grey the region farthest west (West).

Figure 5. Current state of fragmentation of the Atlantic Forest of eastern Brazil, overlaid with the distribution of the genus *Phyllodytes* (darkest gray area) which also encompasses the entire range of *P. luteolus*. Points indicated by the lines and species names are those species with fewer than 10 records and the number of points indicates the number of locations in which they were found. *Phyllodytes tuberculosus* is known from 10 locations, all between *P. acuminatus* in the north and just north of *P.* sp. nov. 1. in the south. Lighter gray indicates the region predicted by the model to be adequate for *Phyllodytes* as in Fig. 3B and D.

Appendix S2. Geographic distribution of all the genera in the subfamily Lophyohylinae (Family Hylidae). Note that *Phytotriades*, the genus phylogenetically closest to *Phyllodytes* is isolated on Venezuela and Trinidad, and species that arose later are widespread in South and Central America and the Caribbean.

Appendix S1. List of the species of *Phyllodytes* and number of locations where recorded, obtained from museums that provided geographic coordinates for modeling and this study. The column State includes the state name and abbreviation.

Species	Records	State
P. brevirostris	1	Paraiba (PB)
P. megatympanum	1	Bahia (BA)
P. punctatus	1	Sergipe (SE)
P. amadoi	1	BA
P. acuminatus	2	Alagoas (AL), Pernambuco (PE)
P. edelmoi	2	AL, PE
P. gyrinaethes	2	AL, PE
P. maculosus	2	BA, Minas Gerais (MG)
P. sp. nov. 1	2	Espírito Santo (ES)
P. sp. nov. 2	1	BA
P. sp. nov. 3	1	BA
P. sp. nov. 4	1	BA
P. kautskyi	3	BA, ES
P. melanomystax	4	BA, SE
P. wuchereri	4	BA
P. tuberculosus	10	BA, SE
P. luteolus	38	AL, BA, ES, MG, PE, PB, Rio de Janeiro (RJ), SE

Figures

Figure 1

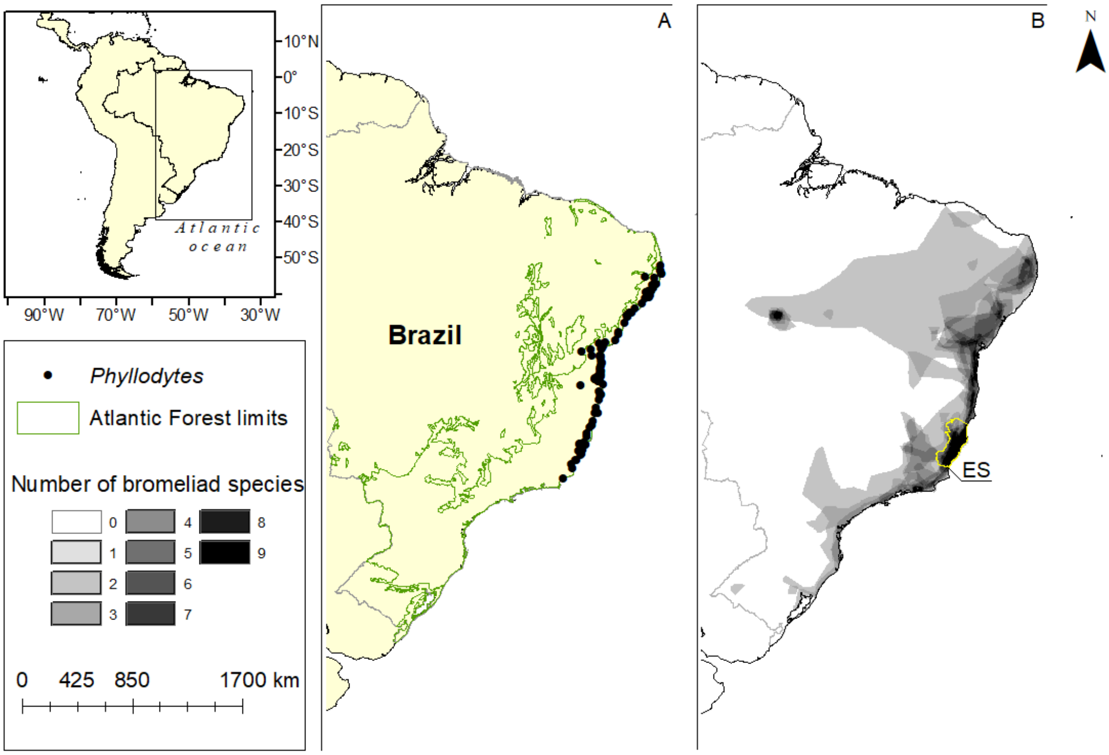
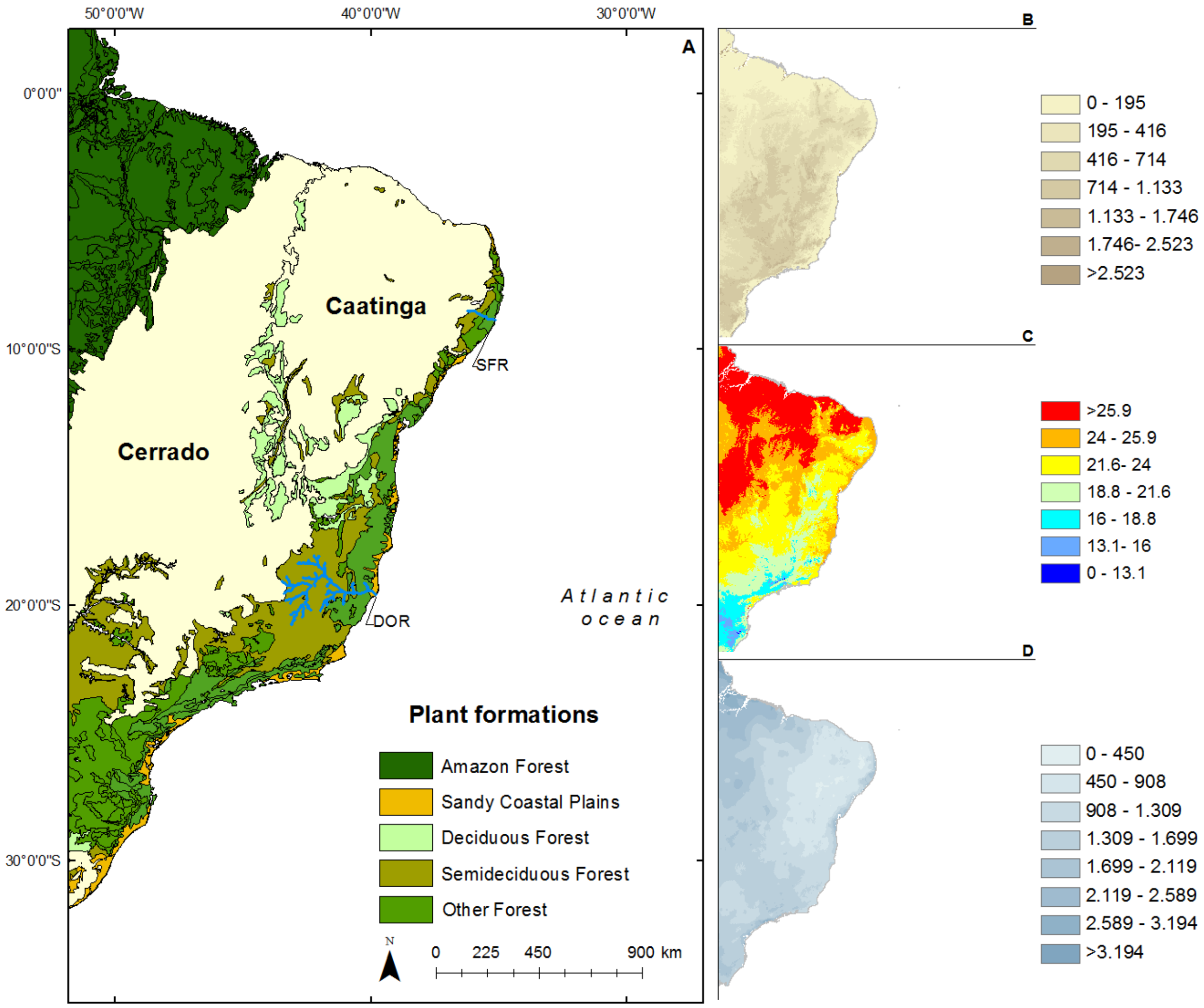
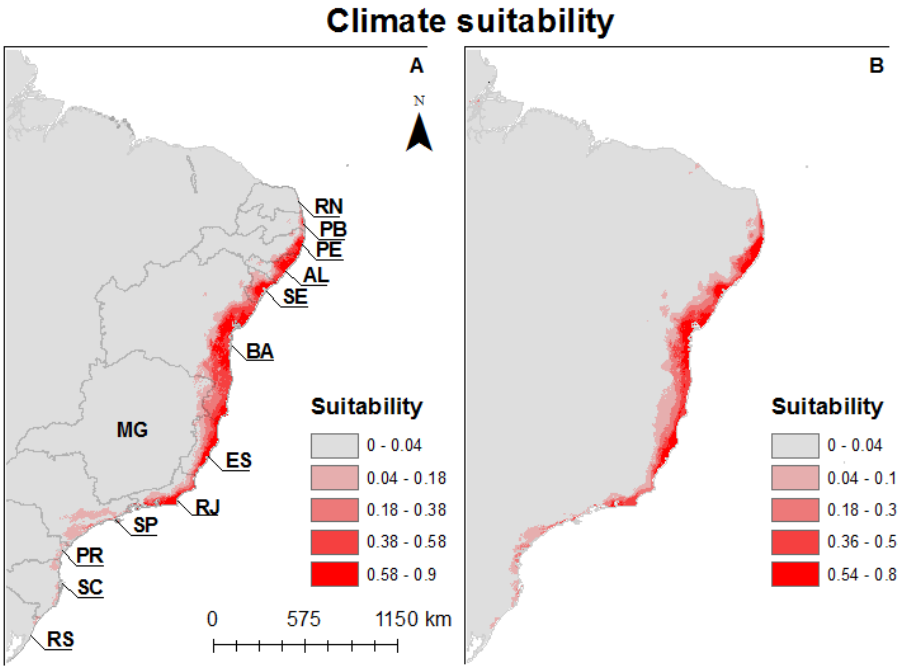


Figure 2



50°0'0"W
40°0'0"W
30°0'0"W
0°0'0"
10°0'0"S
20°0'0"S
30°0'0"S
A
Caatinga
Cerrado
SFR
DOR
Atlantic ocean
Plant formations
Amazon Forest
Sandy Coastal Plains
Deciduous Forest
Semideciduous Forest
Other Forest
N
0 225 450 900 km
B
0 - 195
195 - 416
416 - 714
714 - 1.133
1.133 - 1.746
1.746- 2.523
>2.523
C
>25.9
24 - 25.9
21.6- 24
18.8 - 21.6
16 - 18.8
13.1- 16
0 - 13.1
D
0 - 450
450 - 908
908 - 1.309
1.309 - 1.699
1.699 - 2.119
2.119 - 2.589
2.589 - 3.194
>3.194

Figure 3


Climate suitability

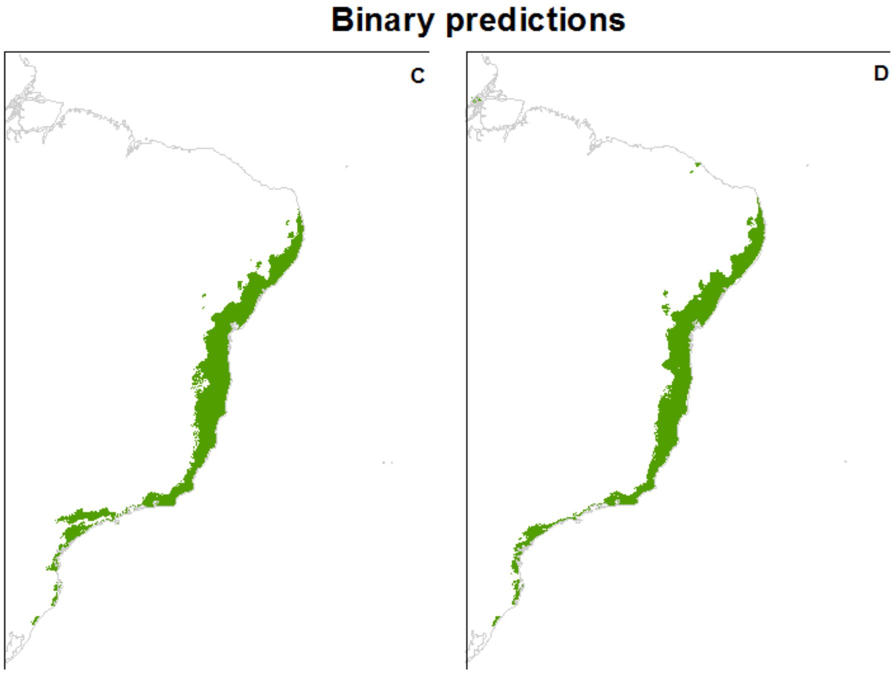
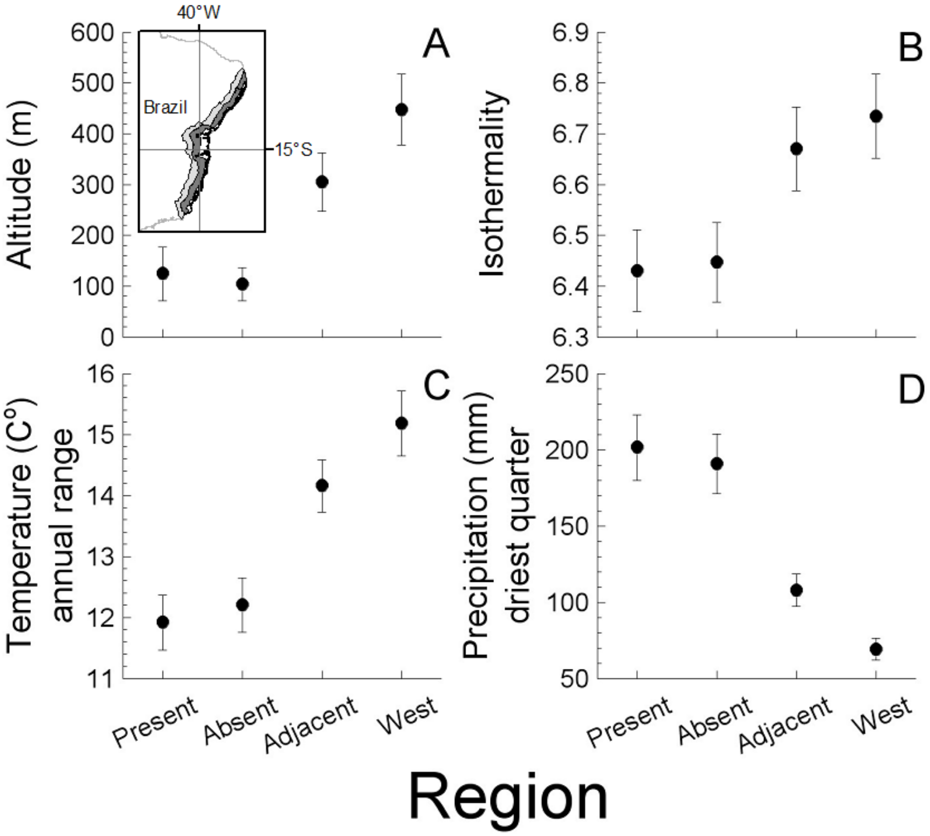
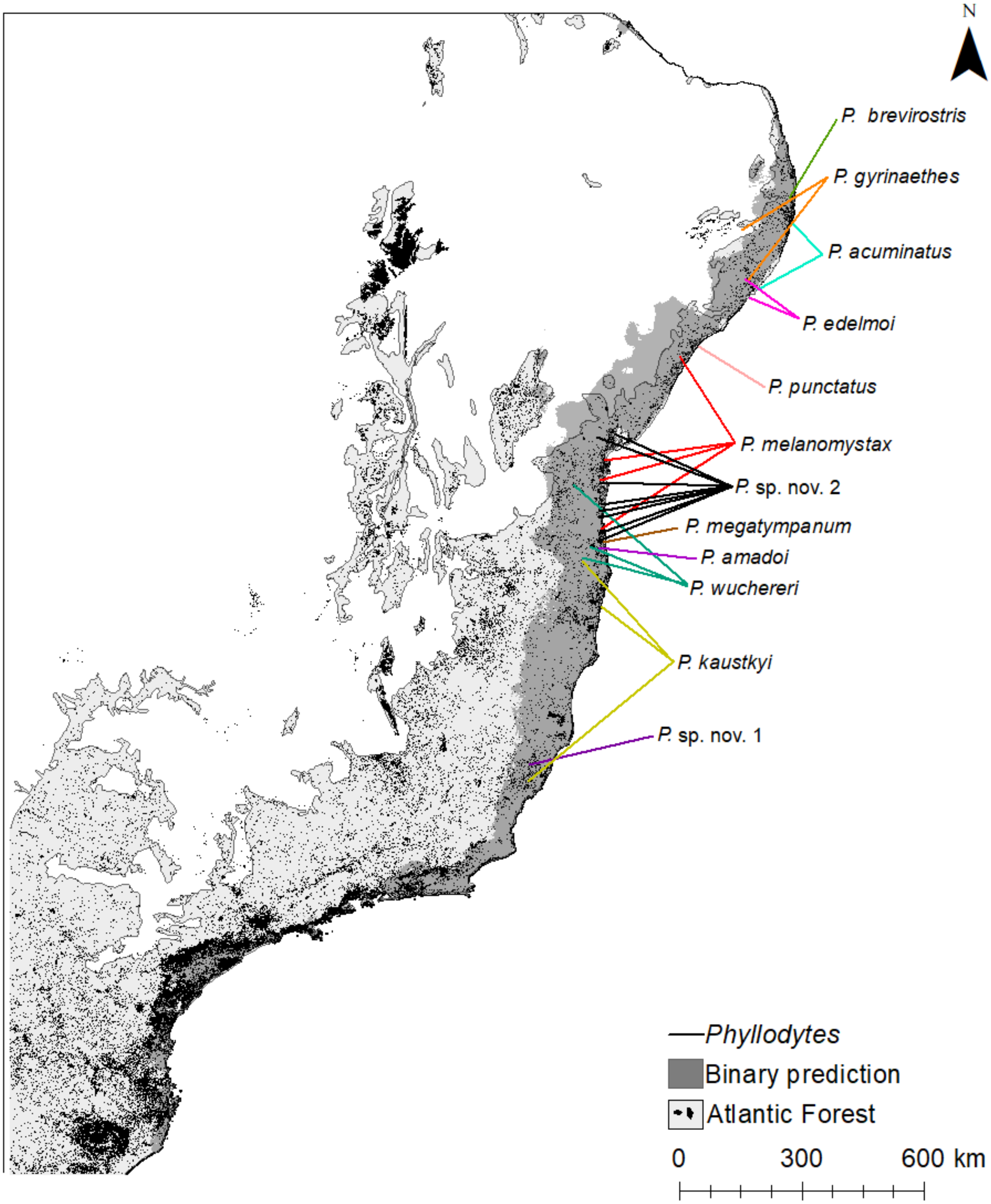

Binary predictions

Figure 4

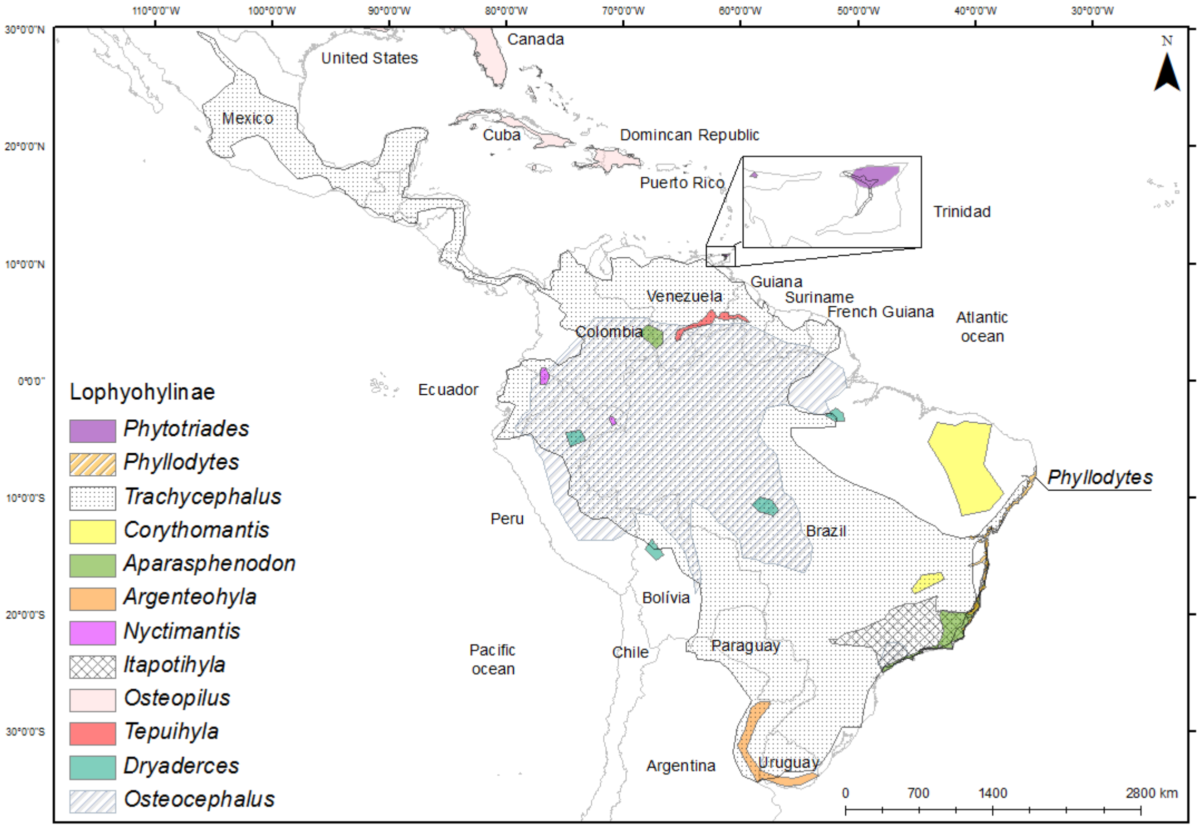


A
B
C
D
40°W
15°S
Brazil
Altitude (m)
0
100
200
300
400
500
600
Isothermality
6.3
6.4
6.5
6.6
6.7
6.8
6.9
Temperature (C°) annual range
11
12
13
14
15
16
Precipitation (mm) driest quarter
50
100
150
200
250
Present
Absent
Adjacent
West
Region

Figure 5


N
P. brevirostris
P. gyrinaethes
P. acuminatus
P. edelmoi
P. punctatus
P. melanomystax
P. sp. nov. 2
P. megatympanum
P. amadoi
P. wuchereri
P. kaustkyi
P. sp. nov. 1
Phyllodytes
Binary prediction
Atlantic Forest
0
300
600 km

Appendix S2


110°0'0"W
100°0'0"W
90°0'0"W
80°0'0"W
70°0'0"W
60°0'0"W
50°0'0"W
40°0'0"W
30°0'0"W
30°0'0"N
20°0'0"N
10°0'0"N
0°0'0"
10°0'0"S
20°0'0"S
30°0'0"S
N
Canada
United States
Mexico
Cuba
Domincan Republic
Puerto Rico
Trinidad
Guiana
Suriname
French Guiana
Venezuela
Colombia
Atlantic ocean
Ecuador
Peru
Brazil
Phyllodytes
Bolívia
Pacific ocean
Chile
Paraguay
Argentina
Uruguay
0
700
1400
2800 km
Lophyohylinae
Phytotriades
Phyllodytes
Trachycephalus
Corythomantis
Aparasphenodon
Argenteohyla
Nyctimantis
Itapotihyla
Osteopilus
Tepuihyla
Dryaderces
Osteocephalus

Plos One

CAPÍTULO 2

The restricted distribution of the bromeliad frogs genus *Phyllodytes*: ghosts of interactions past

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Abstract

Understanding why some groups of organisms currently have small or restricted distributions requires information about climate as well as potential biological interactions. The frog genus *Phyllodytes* comprises 17 poorly-known species that are obligate associates with tank bromeliads and are limited to the Atlantic Forest of eastern Brazil. Here, we use ecological niche modeling to map the distribution of *Phyllodytes* and bromeliads from the past (3 mya, 21 kya, 6 kya) to the present. To evaluate potential exclusion of *Phyllodytes* due to interactions with other bromeliad frogs, we map their distributions to examine their overlap. We predicted that *Phyllodytes* became relegated to marginal habitat due to competition or predation by frogs that are more diverse and more abundant, but that also tend to occur in wetter forests. Our results also indicated that it is unlikely that bromeliads were ever limiting for *Phyllodytes* because they are much more widespread and diverse throughout the region where the frog may have been found and elsewhere. Climate, however, was suitable for *Phyllodytes* at all times, but not in all places. On the other hand, the current and past distributions of other species of bromeliad frogs were more widespread, yet few of those species inhabit regions with the climate extremes in which *Phyllodytes* are found. Also, when bromeliads are present, there is no reason to assume that *Phyllodytes* was unable to inhabit wetter regions under relaxed climatic conditions. Other bromeliad frogs arose more recently than *Phyllodytes* and we suggest that their rapid speciation and association with bromeliads, and often their complex parental care (e.g., Dendrobatidae) and sometimes predatory tadpoles, forced (through competition or predation) *Phyllodytes* into the (climatically) marginal habitats where it is found today.

Introduction

The genus *Phyllodytes* comprises 17 species endemic to lowland Brazilian Atlantic Forest where their distribution is isolated due to harsher surrounding climate [1]. *Phyllodytes* persists in this region due to its obligatory association with tank bromeliads, where they find water [2]. Tank bromeliads are those with a leaf shape and arrangement that allows water to accumulate for extended time intervals thereby providing a continual habitat for the frogs [3]. *Phyllodytes* have been found in 19 bromeliad species, many of which are in the widespread genus *Aechmea* [1, 2, 4, 5, 6, 7, 8, 9]. While *Phyllodytes* are today restricted to the Brazilian Atlantic Forest, they are thought to have arisen along with the sister genus *Phytotriades* in northern South America during the Tertiary (ca. 34.6 mya, [10]). How and why *Phyllodytes* became isolated in eastern Brazil is unclear.

Climate changed dramatically during the 34 million years since the appearance of the genus, although useful climate data for species modeling is only available for up to ~ 5 mya. At the beginning of the Pliocene (ca. 5.33 – 3.6 mya) the climate was warmer and wetter [11, 12] followed by a cooler interval (3.6 – 2.58 mya, [12]). During the Pleistocene (2.58 – 0.01 mya), global climate alternated between warm-wet and cool-dry periods [13]. During the last glacial maximum (Pleistocene, ca. 21 kya) sea level dropped which increased available land area (14, 15, 16, 17). In South America, savannas (*cerrado* and *caatinga*) expanded and the Amazonian and Atlantic forests contracted during the Pleistocene [18, 19, 20, 21, 22, 23]. Sea levels rose again when glaciers retreated due to increasing temperatures during the late Pleistocene [13, 24, 25] and rainforests in South America expanded once again [17].

Biotic interactions can influence distributions [26, 27, 28, 29] and some frog distributions are influenced by competition and predation [30, 31]. Bromeliad frogs only occur where there are tank bromeliads, although as a group, tank bromeliads are essentially omnipresent in tropical and subtropical South America. Thus, while limited within the distributions of tank bromeliads, once present, tank bromeliads do not limit frogs. However, interactions between frogs using tank bromeliads may be important. For example, dart-poison frogs (family *Dendrobatidae*) include species with larvae that prey on eggs and tadpoles of other frog species [32, 33, 34, 35]. Typically, only one viable egg is found in each tank bromeliad and so competition and predation are avoided [36, 37, 38, 39]. Thus, bromeliad frog distributions may have been shaped by competition and predation because of interactions in the bromeliads.

Here, we attempt to determine why and when *Phyllodytes* became isolated in eastern Brazil. Using data from the region currently occupied by the genus, we 1) mapped the potential distribution of *Phyllodytes* expected at three different times in the past (based on their climate regimes) since the Pliocene (ca. 3 mya, 21 kya, 6 kya), 2) placed those possible distributions in the context of potential limitation by the presence of tank bromeliads to test whether bromeliads explain the current distribution, 3) overlay maps of distributions of other frog species that use tank bromeliads to examine whether interactions among frog species may explain the current distribution (emphasizing those that are known to be predatory), and 4) bring this information together to explain the current, limited distribution of the genus *Phyllodytes* and why they are likely to be endangered today.

Materials and methods

Past climate and bromeliads

We began with the current model of climate and geographic limits for *Phyllodytes* [1] and assumed two different models of climatic limits in the past for the genus. First, we assumed that the climate description of region in which *Phyllodytes* is found today describes the true climatic limits (Table 1). We refer to this as the bilateral limits, because we use the climate means and confidence intervals and assume that the frog will not be found outside those limits (above or below). Second, we relax those assumptions and suggest that confidence intervals estimated where frogs are found do not indicate biological limits (but rather are a consequence of the statistics, Table 1). For instance, we suggest that the frog should be able to withstand conditions with greater rainfall and cooler temperatures and we refer to this scenario as the unilateral limits for the frog.

Table 1. Climatic limits used in this study. Bilateral limits are based on modeled climate suitability and unilateral limits are based on bioligically reasonable values (modified from Mageski et al., in review). [a]The infinity symbol in the unilateral limits column indicates that there was no limit imposed in that direction.

Climatic variables	Bilateral Limits	[a]Unilateral Limits
Max Temperature of Warmest Month (°C)	27 - 30	27 – ∞
Min Temperature of Coldest Month (°C)	16 - 22	16 – ∞
Temperature Annual Range (°C)	6 - 13	∞ - 28
Annual Precipitation (mm)	751 – 1400	751 – ∞
Precipitation of Driest Quarter (mm)	93 - 148	93 – ∞

We used ArcMap 10 [40, 41] to map the current distribution of the genus *Phyllodytes* and bromeliads (Fig. 1A and B, respectively) to place both in the same biogeographical context. We assume that *Phyllodytes* can use any tank bromeliad species that is known to be used by any other frog species [3]. Thus, we gathered information for any tank bromeliads that are similar to those used by *Phyllodytes*, by searching on Species Link [42] and Global Biodiversity Information Facility [43].

We obtained bioclimatic data from Ecoclimate, which are standardized in space and time using Atmosphere-Ocean Global Circulation Models (AOGCMs, [44, 45). Using 0.5º resolution, we selected uncorrelated variables that were modeled to be important for *Phyllodytes* [1], namely maximum temperature of warmest month (Bio 5), minimum temperature of coldest month (Bio 6), annual range in temperature (Bio 7), annual precipitation (Bio 12), and precipitation of driest quarter (Bio 17).

We used bathymetry and orography models for South America from ETOPO1 Bedrock [46] and the curve of sea level change [13] to plot sea level variation and exposed continental shelf in each time period. We converted these raster maps to polygons using the raster package [47] in R 3.3.0 [48] and use as a mask for climatic rasters to eliminate ocean cells and considering variations in continental shelf in all considered periods before modeling. Further, all raster layers were cropped to South America (-100º to -30º longitude, -60º to 30º latitude) as a landscape, using raster package in R. We use the Community Climate System Model (CCSM) for modeling frogs and bromeliads distributions during the Pliocene, Pleistocene (Last Glacial Maximum – LGM), mid-Holocene and present. CCSM is a single AOGCM with variables for all periods in the past in Ecoclimate [44].

We used climate distribution limits for *Phyllodytes* that provide a mean and 95% confidence interval estimated within the range of the genus [1]. Those limits, by definition, are bilateral, while frog biology suggests that some of those limits may be unilateral. For example, rainfall may limit frogs at the low end, but not necessarily at the high end. Also, the temperature limit may be contextual in that higher temperatures can occur if rainfall is also more constant. Thus, we use this reasoning to develop two models to examine changing distributions over time. The first, using bilateral limits (hereafter bilateral) as a consequence of estimating climate within the frog distribution and the relaxed limits in which there are no upper limits to rainfall and temperature (hereafter unilateral limits). While *Phyllodytes* may have used other bromeliads over time and in its former range, for modeling we simply use the distributions of all bromeliad species in which any bromeliad-using frog has been found [3, 49]. We then extracted climate within the ranges of tank bromeliads and, based on those conditions, mapped bilateral and unilateral climate limits over time and calculated the extent of the predicted ranges for frogs and bromeliads in each period using the raster package in R.

Biological interactions with other bromeliad-using frog species

We used published information [50, 51, 52, 53, 54, 55, 56, 57] and our field data to estimate geographic distributions of other bromeliad frog species. Results of this search were used to estimate the range and number of bromeliad frog species by ecoregion [58] in South America.

Results

Past climate and bromeliads

Based on the current climate conditions where *Phyllodytes* are found, the model predicts additional areas where it may occur and the unilateral model predicts a more widespread distribution than the bilateral (Figs 1 and 2). The bilateral model tends to have fragments from which dispersal would not allow frogs to reach one fragment from the other, and thus does not show how the frogs might have gotten to eastern Brazil. The unilateral model, on the other hand, predicts a large contiguous area in northern South America that would have been possible to reach eastern Brazil. However, the models contrasted mainly in northern more humid regions of South America (e.g. Amazon forests) in which the unilateral model predicted a greater extent of suitable climate than those predicted by the bilateral model (Fig 2).

Fig 1. Geographical distribution of the genus of *Phyllodytes* and genus of bromeliads in which they have been found.

Fig 2. Climate suitability predictions over time for *Phyllodytes*. The first row is based on climate modeling alone (bilateral limits) and the second row is based on the biologically reasonably unilateral limits. The third row shows the changing tank bromeliad distribution.

Predictions indicate that suitable climate for *Phyllodytes* increased during warm and wet conditions, mainly after the last glacial maximum (Fig 2). During the Pleistocene (last glacial maximum), the range may have increased in northern and eastern South America, in part due to the continental shelf that was exposed by the receding sea level (Fig 2B). As temperature increased and ice melted during mid-Holocene, suitable climate increased in northern South America once again and other regions became suitable in eastern Brazilian coast, creating a continuum across predicted range (Fig 2). Suitable climate continued to increase in northern South America and, especially, in eastern Brazil after mid-Holocene shaping the current potential distribution for *Phyllodytes* (Fig 2).

The presence of bromeliads is unlikely to have ever limited the distribution of *Phyllodytes*. The distribution of *Phyllodytes* is a small subset of the region in which tank bromeliads are found (Fig 1). Bromeliads were very widespread in South and Central America and apparently were always more widespread than *Phyllodytes* in all considered periods (Fig 2).

Competition and predation

Of the 166 species of bromeliad frogs of the Neotropical region, 146 (88%) inhabit tropical rainforests, and majority of species (71, 49%) belongs to Hylidae, followed by Dendrobatidae (43, 29%, S1 Appendix). Although the distribution of *Phyllodytes* is within the distribution of a few potential competitors, *Phyllodytes* is not found where there are many other bromeliad frog species (Fig 3). Of the 129 potential competitor and predator frog species, 22 (17%) overlap with *Phyllodyte*s. The distributions of the eight species with carnivorous tadpoles are entirely exclusive of the distribution of *Phyllodytes* (S1 Appendix). Most species of bromeliad frogs whose distributions overlap that of *Phyllodytes* (21, 95%) are much more widespread and in more humid forests (S1 Appendix). Also, *Phyllodytes* was only once found with another bromeliad frog (*Dendropsophus bromeliaceus*) in the same patch (but not in the same plant (present study).

Fig 3. The distribution of the other bromeliad frog species that potentially compete with or prey on (as tadpoles) *Phyllodytes* in South America.

The number of species varies from none (white) to eight (darkest grey) where the distributions overlap.

All species of bromeliad frogs (whose origins have been estimated) date from the Tertiary (65 – 2.5 mya), including those with carnivorous tadpoles, and so they arose after *Phyllodytes*, and only three species of *Pristimantis* arose before *Phyllodytes* (S1 Appendix).

Discussion

We demonstrate that the distribution of *Phyllodytes* spp., if only limited by bromeliads, could have been much larger distribution than it is today, especially if we relax conditions of the climate in which they are found today [1]. This possibility implies that other, biological [27, 59, 60, 61, 62], processes are likely to have relegated the genus to its current distribution. *Phyllodytes* may have originated in association with bromeliads in moist broadleaf forests of northern South America [10], and as bromeliads expanded their distributions, *Phyllodytes* is likely to have followed. Soon thereafter, other species of frogs began to be associated with bromeliads, thereby bringing several species into contact. Once in contact, potentially limiting interactions began, including predation and competition for breeding sites. We propose that *Phyllodytes*, perhaps due to their small size or simply due to the characteristics of their early association with bromeliads (about which more below), withstood more xeric conditions, while the other frogs, arising in more humid conditions, favored wetter forests. Thus, over time, *Phyllodytes* was forced into marginal, drier habitats as the several other, newly arisen, bromeliad frog species together occupied the wetter regions. Also, it is possible that the early conditions that favored *Phyllodytes* were marginal, drier in which the bromeliads were the only source of water. In this case, perhaps *Phyllodytes* would have expanded its distribution to include any region with bromeliads, but it was limited by the presence of better competitors or predators.

The regions with conditions similar to that where *Phyllodytes* is found today have been quite limited over time (Fig 2A). The frogs would have been unable to reach the regions outside of South America (lack of corridors, land bridges, continuity of distribution, etc.), and so they need not be considered further. When we relax the climate limits in South America, regions aside from that in which *Phyllodytes* is found today, all have a variety of other species of bromeliad frogs (Fig 2B, 3). These frogs include species with parental care and others with predatory tadpoles. Thus, the combined effect of these interactions may have simply eliminated *Phyllodytes* wherever these other species are found. The end result of this process leaves *Phyllodytes* in its current distribution.

Past climate and bromeliads

In general, climate models suggested that the distribution of *Phyllodytes* would have been able to increase during warm and wet periods and have decreased when climate was drier (e.g. LGM). Our results also indicated the smallest potential range during the LGM (Fig. 2), similar to that of other studies for other organisms. For example, six North American plant species had the smallest distributions during the LGM [63]. Another example is that forest-dependent bee species in South America have been increasing their range since the LGM [64]. The lack of appropriate climate in the Pliocene, in both the bilateral and unilateral scenarios, suggests two possibilities. First, that the genus had not yet reached eastern Brazil. Second, that it was already in eastern Brazil, and the climate limits where it is found today do not, in fact, limit the frogs. The former case implies that corridors of some sort appeared more recently than the Pliocene. The latter case implies that interactions among frogs (and possibly other predators, parasites, competitors) are even more likely to have relegated the genus to its current distribution.

Two routes for biotic interchanges between the Amazon and Atlantic Coastal rainforests were available several times in the past. The first (south-eastern—north-western) would have connected the southern Amazon to the southern Atlantic Forest across the present-day *Cerrado* (Brazilian Savannas). The second possible route (north-eastern) connected northeastern Amazon to the northern Atlantic Forest, across the present-day *Caatinga* (more xeric savanna; [23]) The first route was important for some frogs of the genera *Dendrophryniscus* and *Amazophrynella* [18, 65, 66]. Because fossil data, older climatic data and a phylogeographic analysis for *Phyllodytes* are all unavailable, we do not know the route by which *Phyllodytes* dispersed from northern South America to the Atlantic Forest. We propose two alternative hypotheses for dispersal. First, that frogs arrived in eastern Brazil more than 3 mya, because climate changed several times since the origin of the genus and older connections between Amazon and Atlantic Forest may allowed the dispersion. Also, in the Pliocene, there were scattered regions in eastern Brazil that were appropriate climatically for the frogs. Second, because during the Pliocene, the area that could have been occupied by *Phyllodytes* was very small and isolated, frogs arrived after the Pleistocene, because other studies have shown connections between the Amazonian and Atlantic forests after that time. We favor the first hypothesis because it suggests that *Phyllodytes* arrived early in eastern Brazil, where it then had ample time to have speciated into the current 17 species found today (perhaps due to continual fragmentation and isolation of populations due to changing climate). The second hypothesis requires a much more recent arrival eastern Brazil, with little time for speciation. The ghost of interactions past [27] is due to the current isolation of the Atlantic Forest from the Amazonian Forest and the few species of competitive or predatory frogs found in the current range of *Phyllodytes*.

Clearly, bromeliads never limited frog distributions, even though they are obligatory for the frogs. Tank bromeliad distributions have always been much greater, encompassing climatic conditions much more variable than those experienced by *Phyllodytes* (Fig 2C). This suggests that bromeliads (and with climate) did not constrain *Phyllodytes* to the xeric conditions in which it is found today.

Competition and predation

Most bromeliad frog species, including those with carnivorous tadpoles, inhabit rainforests (Amazon and Atlantic Forest). Obligate bromeliad frogs are known to apparently avoid each other in bromeliads [4, 8, 67, 68, 69, 70]. This suggests that the distributions of many bromeliad frogs (in addition to *Phyllodytes*) may have been influenced by interactions among species. Most bromeliad frog species originated more recently than *Phyllodytes* (S1 Appendix) which suggests that when *Phyllodytes* arose through the end of Tertiary, only intraspecific competition for bromeliads was important. Subsequently, more than 90 new bromeliad frog species appeared, when interspecific interactions, with several species, became more common. We suggest that during this time, *Phyllodytes* was eliminated from the areas with many other species of frogs, and it continued in areas with little or no competition or predation – the more xeric regions that are inhospitable to rainforest (often larger) frogs. This kind of displacement has been demonstrated for a variety of organisms [71]. For example, big cats in the subfamily Felinae (including the cougar, *Feliz concolor*, and the Eurasian puma, *Puma pardoides*) were displaced from Eurasia, ending up extinct (the latter) or in the Americas (the former), due to expansion by big cats in the subfamily Pantherinae (including the leopard, *Panthera pardus*) during the Pleistocene [72]. Also, the post Pleistocene distribution of hedgehogs (*Erinaceus* spp.) in Europe were probably a result of mutual exclusion by competition between species [73].

We recognize the speculative nature of this study, but without fossils and without data for weather farther back in time, any attempt to determine the causes of current species limitations will be speculative. Nonetheless, we have shown that climate is unlikely to force the frog into marginal conditions, because considering climate alone, nothing prevents the frog from existing in less extreme conditions. Since *Phyllodytes* is likely to have arisen close to its sister-genus *Phytotriades*, the genus would have had to have found its way to eastern Brazil in regions with more moderate climates. Also, while the association with bromeliads is obligatory, it is not limiting because bromeliads have much larger distributions than does the frog. In the light of these observations, biological interactions are likely to have forced the frogs into their current distribution. While it is also possible that parasites are also part of the picture, and density-dependent interactions with their hosts (this might be true for all bromeliad frogs) may have also favored lower densities or non-overlapping distributions. Further study can examine that possibility. One consequence of being relegated to northeastern Brazil is that the current distribution is surrounded by more inhospitable conditions. Also, the entire region in which it is found today is highly fragmented due to agriculture and a growing human population. This poorly understood genus of frogs, once relegated to an isolated and inhospitable distribution due to biological interactions with other frogs, is now likely to be endangered due to biological interactions of another kind – with humans.

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Figure 1

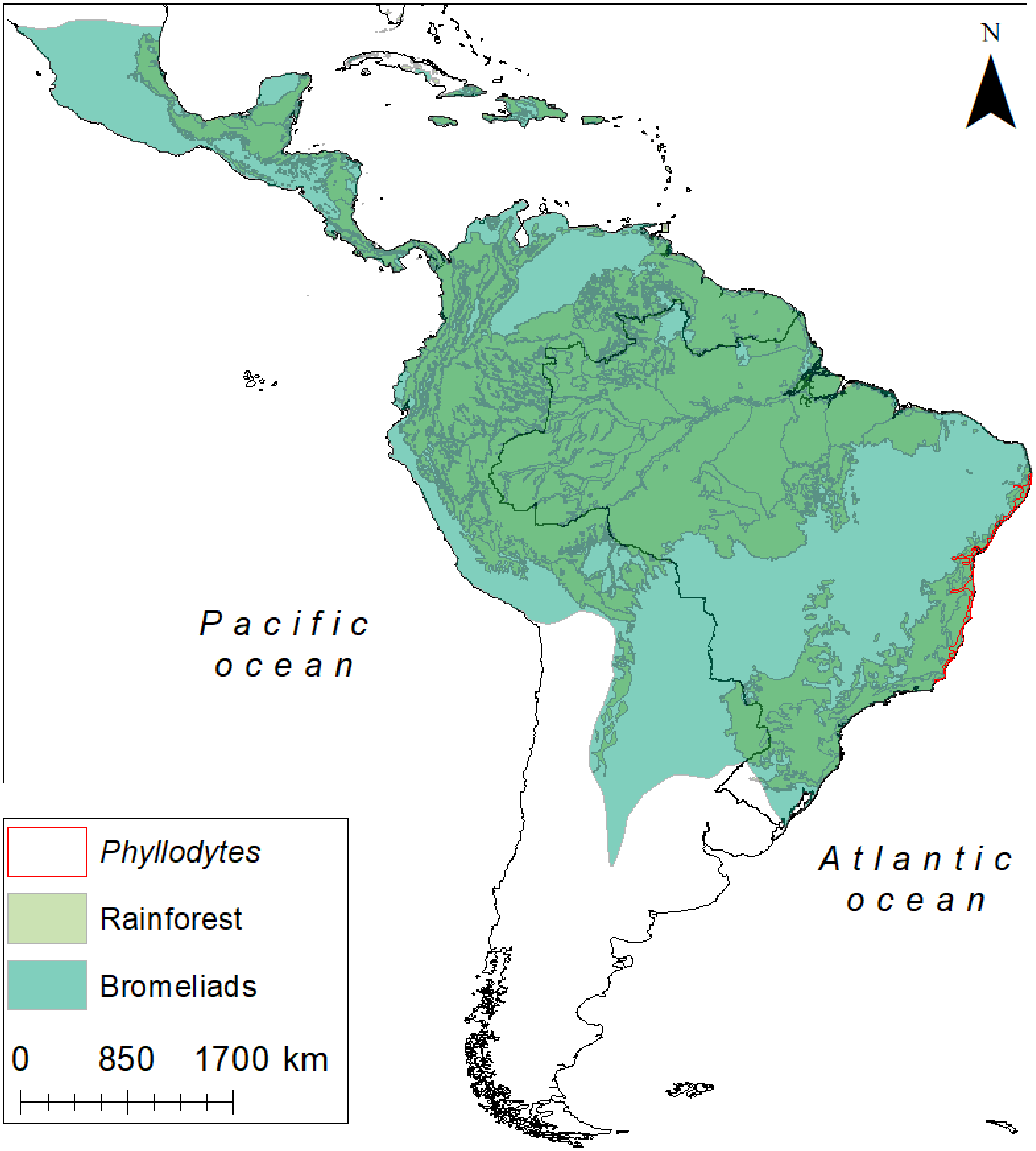

N
Pacific ocean
Atlantic ocean
Phyllodytes
Rainforest
Bromeliads
0
850
1700 km

Figure 2

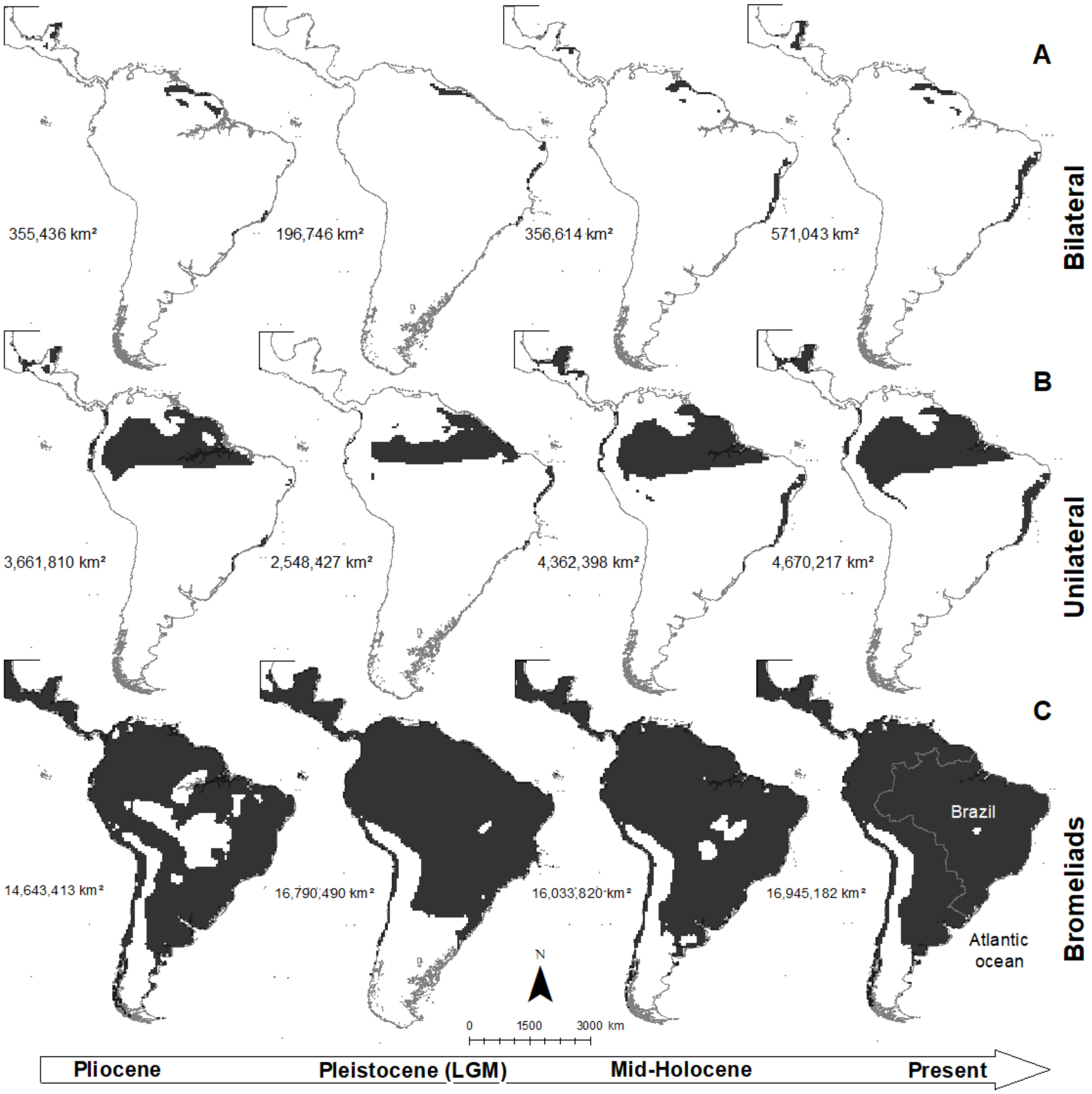
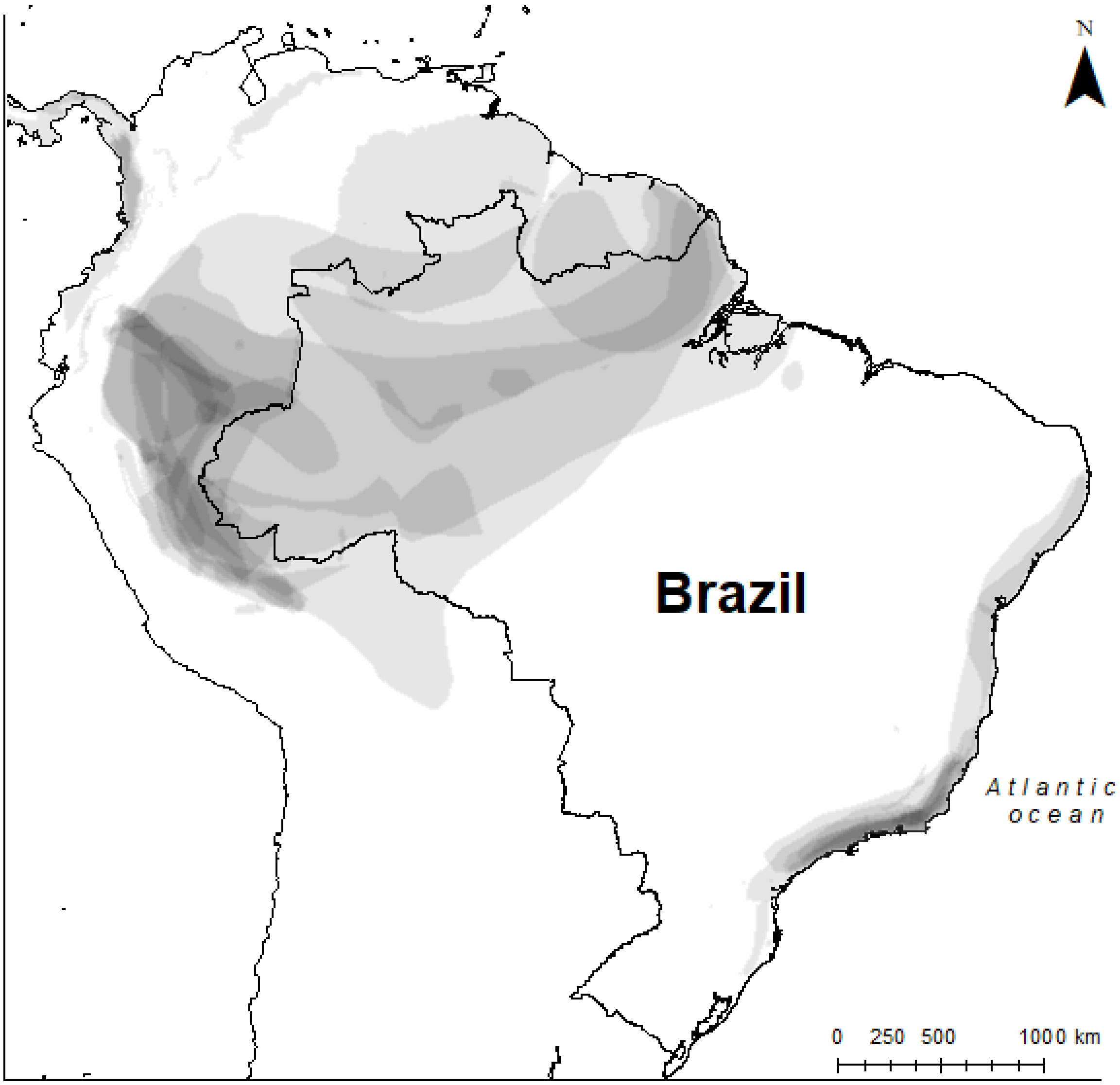

A
Bilateral
355,436 km²
196,746 km²
356,614 km²
571,043 km²
B
Unilateral
3,661,810 km²
2,548,427 km²
4,362,398 km²
4,670,217 km²
C
Bromeliads
14,643,413 km²
16,790,490 km²
16,033,820 km²
16,945,182 km²
Brazil
Atlantic ocean
N
0
1500
3000 km
Pliocene
Pleistocene (LGM)
Mid-Holocene
Present

Figure 3



Supporting information

S1 Appendix. Bromeliad frogs of Neotropical region and their ages. Age of the species were presented in million years ago (mya) or unknown (-) according to Isaac et al. [74] and Rosindell et al. [75]. Continent are CA, Central America, NA, North America and SA, South America. Ecoregions are DXS, Deserts and Xeric Shrublands, DBF, Dry Broadleaf Forests, FGS, Flooded Grasslands Savannas, GSS, Grasslands, Savannas and Shrublands, MBF, Moist Broadleaf Forests, MGS, Montane Grasslands and Shrublands, SCF, Subtropical Conifer Forest, SCP, Sandy Coastal Plain. Tadpole, 0, not carnivorous, 1, carnivorous, -, unknown. *, species in which distribution overlapped with *Phyllodytes*.

Family Species	Continent	Ecoregions	Tadpole
Aromobatidae			
Allobates bromelicola (16.6)	SA	MBF	-
Anomaloglossus beebei (12.9)	SA	MBF	1
Bufonidae			
Dendrophryniscus berthalutzae (13.3)	SA	MBF	-
Dendrophryniscus brevipollicatus (13.3)*	SA	MBF, SCP	-
Dendrophryniscus carvalhoi (13.3)*	SA	MBF	-
Dendrophryniscus krausae (-)	SA	MBF	-
Dendrophryniscus organensis (-)	SA	MBF	-
Dendrophryniscus stawiarskyi (13.3)*	SA	MBF	-
Frostius pernambucensis (30.4)*	SA	MBF, DXS, SCP	0
Melanophryniscus alipioi (-)	SA	MBF	-
Melanophryniscus biancae (-)	SA	MBF	-
Melanophryniscus milanoi (-)	SA	MBF	-
Melanophryniscus setiba (-)*	SA	MBF, SCP	-
Melanophryniscus vilavelhensis (-)	SA	MBF	-
Melanophryniscus xanthostomus (-)	SA	MBF	-
Brachycephalidae			
Ischnocnema venancioi (11.8)*	SA	MBF	-
Centrolenidae			
Cochranella riveroi (11)	SA	MBF	-
Craugastoridae			
Pristimantis aureolineatus (-)	SA	MBF	-
Pristimantis eugeniae (44.2)	SA	MBF	-
Pristimantis juanchoi (21.8)	SA	MBF	-
Pristimantis lacrimosus (44.2)	SA	MBF	-

Pristimantis platydactylus (-)	SA	MBF	-
Pristimantis urichi (36.1)	CA	MBF	-
Pristimantis wagteri (-)	SA	MBF	-
Pristimantis waoranii (-)	SA	MBF	-
Dendrobatidae			
Andinobates abditus (14)	SA	MBF	-
Andinobates altobueyensis (14)	SA	MBF	-
Andinobates bombetes (14)	SA	DBF	-
Andinobates daleswansoni (-)	SA	DBF	-
Andinobates dorisswansonae (-)	SA	MBF	-
Andinobates fulguritus (14)	SA; CA	MBF	-
Andinobates minutus (14)	SA; CA	MBF	1
Andinobates opisthomelas (14)	SA	MBF, DBF	-
Andinobates viridis (14)	SA	MBF	-
Andinobates virolinensis (14)	SA	MBF, DBF	-
Colostethus ruthveni (12.9)	SA	DBF	-
Dendrobates auratus (7.2)	CA; SA	MBF	1
Dendrobates benedicta (-)	SA	MBF	-
Dendrobates defleri (-)	SA	MBF	-
Dendrobates igneus (14)	SA	MBF	1
Dendrobates leucomelas (7.2)	SA	MBF, GSS	1
Dendrobates summersi (-)	SA	MBF	-
Dendrobates tinctorius (7.2)	SA	MBF	1
Excidobates condor (-)	SA	MBF	-
Excidobates mysteriosus (-)	SA	MBF	-
Minyobates steyermarki (16.8)	CA; SA	MBF	-
Oophaga arborea (9.9)	CA	MBF	-
Oophaga granulifera (9.9)	CA	MBF	0
Oophaga histrionica (9.9)	SA	MBF	0
Oophaga lehmanni (9.9)	SA	MBF	0
Oophaga occultator (9.9)	SA	MBF	-
Oophaga pumilio (9.9)	CA	MBF	0
Oophaga speciosa (9.9)	CA	MBF	0
Oophaga sylvatica (9.9)	SA	MBF	-
Phyllobates lugubris (9.9)	CA	MBF	0
Phyllobates vittatus (9.9)	CA	MBF	0
Ranitomeya amazonica (14)	SA	MBF	-
Ranitomeya cyanovittata (-)	SA	MBF	-
Ranitomeya fantastica (14)	SA	MBF	0
Ranitomeya flavovittata (14)	SA	MBF	-
Ranitomeya imitator (14)	SA	MBF	-
Ranitomeya sirensis (14)	SA	MBF	-
Ranitomeya toraro (-)	SA	MBF	-
Ranitomeya uakarii (-)	SA	MBF	-
Ranitomeya vanzolinii (14)	SA	MBF	-
Ranitomeya variabilis (14)	SA	MBF	1
Ranitomeya ventrimaculata (14)	SA	MBF	1

Ranitomeya yavaricola (-)	SA	MBF	-
Hylidae			
Anotheca spinosa (4.8)	CA	MBF	0
Aparasphenodon arapapa (-)*	SA	MBF	-
Boana liliae (-)	SA	MBF	-
Bokermannohyla astartea (22.8)*	SA	MBF	-
Bromeliohyla bromeliacia (5.4)	NA; CA	MBF	-
Bromeliohyla dendroscarta (5.4)	NA	MBF	0
Dendropsophus bromeliaceus (-)*	SA	MBF	-
Ecnomiohyla minera (18)	CA	SCF	-
Ecnomiohyla sukia (-)	CA	MBF	-
Flectonotus fitzgeraldi (12.8)	CA; SA	MBF, DXS, SCP	-
Flectonotus pygmaeus (12.8)	SA	MBF, DXS	0
Fritziana fissilis (12.8)*	SA	MBF	-
Fritziana goeldii (12.8)*	SA	MBF, GSS	0
Fritziana ohausi (12.8)*	SA	MBF	0
Fritziana tonimi (-)*	SA	MBF	0
Gastrotheca antoniiochoai (-)	SA	MBF	-
Gastrotheca fissipes (31.5)*	SA	MBF, DXS	-
Gastrotheca megacephala (-)*	SA	MBF, SCP	-
Gastrotheca microdiscus (31.5)*	SA	MBF, SCP	-
Gastrotheca ochoai (31.5)	SA	MBF, MGS	-
Gastrotheca plumbea (31.5)	SA	MBF, MGS	-
Gastrotheca prasina (-)	SA	MBF	-
Isthmohyla melacaena (-)	CA	MBF	-
Isthmohyla picadoi (10.2)	CA	MBF	-
Isthmohyla zeteki (10.2)	CA	MBF	0
Ololygon alcatraz (29.7)	SA	MBF	-
Ololygon arduous (29.7)*	SA	MBF	-
Ololygon atrata (29.7)	SA	MBF	-
Ololygon belloni (-)	SA	MBF	-
Ololygon cosenzai (-)	SA	GSS	-
Ololygon faivovichi (-)	SA	MBF	-
Ololygon insperatus (-)	SA	GSS	-
Ololygon littoreus (29.7)	SA	MBF	-
Ololygon melloi (29.7)	SA	MBF	-
Ololygon peixotoi (-)	SA	MBF, GSS	-
Ololygon perpusilla (29.7)*	SA	MBF	0
Ololygon tupinamba (-)	SA	MBF	-
Ololygon v-signata (29.7)*	SA	MBF	-
Osteocephalus buckleyi (22.1)	SA	MBF	-
Osteocephalus castaneicola (-)	SA	MBF	-
Osteocephalus deridens (22.1)	SA	MBF	0
Osteocephalus fuscifacies (22.1)	SA	MBF	-
Osteocephalus heyeri (22.1)	SA	MBF	-
Osteocephalus leoniae (22.1)	SA	MBF	-
Osteocephalus oophagus (22.1)	SA	MBF	0

Osteocephalus planiceps (22.1)	SA	MBF	-
Osteopilus crucialis (16.2)	CA	MBF	0
Osteopilus marianae (16.2)	CA	MBF	0
Osteopilus ocellatus (16.2)	CA	MBF	0
Osteopilus wilderi (16.2)	CA	MBF	0
Phyllodytes acuminatus (34.6)	SA	MBF, SCP	-
Phyllodytes amadoi (34.6)	SA	MBF, SCP	-
Phyllodytes brevirostris (34.6)	SA	MBF, SCP	-
Phyllodytes edelmoi (34.6)	SA	MBF, SCP	-
Phyllodytes gyrinaethes (34.6)	SA	MBF, SCP	-
Phyllodytes kautskyi (34.6)	SA	MBF, SCP	-
Phyllodytes luteolus (34.6)	SA	MBF, SCP	-
Phyllodytes maculosus (34.6)	SA	MBF, SCP	-
Phyllodytes megatympanum (-)	SA	MBF, SCP	-
Phyllodytes melanomystax (34.6)	SA	MBF, SCP	-
Phyllodytes punctatus (34.6)	SA	MBF, SCP	-
Phyllodytes tuberculosus (34.6)	SA	MBF, SCP	-
Phyllodytes wuchereri (34.6)	SA	MBF, SCP	-
Phyllodytes sp. nov. 1 (-)	SA	MBF, SCP	-
Phyllodytes sp. nov. 2 (-)	SA	MBF, SCP	-
Phyllodytes sp. nov. 3 (-)	SA	MBF, SCP	-
Phyllodytes sp. nov. 4 (-)	SA	MBF, SCP	-
Phytotriades auratus (34.6)	CA; SA	MBF	-
Tepuihyla exophthalma (-)	SA	MBF	-
Trachycephalus cunauaru (-)	SA	MBF	-
Trachycephalus helioi (-)	SA	MBF	-
Microhylidae			
Chiasmocleis antenori (16.3)	SA	MBF	0
Chiasmocleis tridactyla (16.3)	SA	MBF	-
Ctenophryne carpish (-)	SA	MBF	-
Leptodactylidae			
Crossodactylodes bokermanni (12.7)*	SA	MBF	-
Crossodactylodes itambe (-)	SA	MBF	-
Crossodactylodes izecksohni (12.7)*	SA	MBF	-
Crossodactylodes pintoi (12.7)	SA	MBF	-
Crossodactylodes septentrionalis (-)*	SA	MBF	-
Eleutherodactylidae			
Diasporus diastema (21.2)	CA	MBF	-
Diasporus vocator (21.2)	CA	MBF	-
Eleutherodactylus amplinympha (31.6)	CA	MBF	-
Eleutherodactylus auriculatoides (31.6)	CA	SCF	-
Eleutherodactylus bakeri (17.7)	CA	MBF	-
Eleutherodactylus cochranae (31.6)	CA	MBF	-
Eleutherodactylus corona (19.6)	CA	MBF	-
Eleutherodactylus flavescens (31.6)	CA	MBF	-
Eleutherodactylus fowleri (31.6)	CA	MBF, DBF	-
Eleutherodactylus gryllus (31.6)	CA	MBF	-

Eleutherodactylus guantanamera (31.6)	CA	MBF	-
Eleutherodactylus heminota (-)	CA	MBF, DBF	-
Eleutherodactylus ionthus (31.6)	CA	MBF	-
Eleutherodactylus jamaicensis (-)	CA	MBF	-
Eleutherodactylus lamprotes (9.36)	CA	MBF	-
Eleutherodactylus portoricensis (31.6)	CA	MBF	-
Eleutherodactylus schwartzi (31.6)	CA	MBF	-
Eleutherodactylus varians (31.6)	CA	MBF, DBF, FGS	-
Eleutherodactylus wetmorei (31.6)	CA	MBF, DBF, SCF	-

Herpetologica

CAPÍTULO 3

Impending climate change will endanger the eastern Brazilian endemic bromeliad frog genus *Phyllodytes*

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RRH: MAGESKI ET AL.— FUTURE DISTRIBUTION AND POTENTIAL EXTINCTION IN *PHYLLODYTES*

ABSTRACT: Frogs are very sensitive to climate due to dispersal, physiological and reproductive limitations. Because of those limitations, several frog species may be at risk of extinction due to climate change. Species will only persist if the future distribution of regions with appropriate climates are available into which the organisms can easily disperse and understanding this process should be a conservation priority. Here, we use niche modeling to: 1) predict the effects of future climate change on the distribution of the genus *Phyllodytes*, 2) Predict which of the several species of *Phyllodytes* are likely to go extinct before the end of the century, and 3) identify potentially climatically stable areas within the range of the genus that may be essential for the conservation and persistence of *Phyllodytes*. We model present and future climate considering two scenarios 1) increase 0.3°-1.7°C (minimal temperature increase) and 2) 2.6°-4.8°C (maximal increase), we modeled the distribution of *Phyllodytes* using maximum entropy. Models indicate that the distribution of *Phyllodytes* will be drastically reduced as a consequence of increasing temperature. Northern members of the genus are likely to become extinct in less than 100 years. With these results in mind, we suggest that the entire genus is endangered with extinction. If the genus persists, it will comprise isolated populations in the state of Espírito Santo. Whether the genus persists will require concerted research and analysis to determine whether populations will have regions with suitable climate and whether political willpower will insure protection and conservation measures.

Key words: Frogs; Atlantic Forest; Distribution; Conservation; Ecological niche modeling; MaxEnt

ORGANISMS today are confronted with climate change and before the end of this century temperature is expected to increase not be evenly across the planet, which will be accompanied by rising sea levels and changing rainfall patterns (IPCC 2014; Chou et al. 2014; DeConto and Pollard 2016; Le Bars et al. 2017). As climate changes, phenology, biological interactions, species distributions and ecosystem functioning will also change (Parmesan 2006; Williams et al. 2007; Raxworthy et al. 2008; Lemes and Loyola 2013). For example, studies in the Artic find that some species, including caribou (*Rangifer tarandus*) and polar bears (*Ursus maritimus*), are declining in abundance due to melting ice (Stirling and Parkinson 2006; Post and Forchhammer 2008; Post et al. 2009). In South America, some widespread species, such as the grasshopper (*Tropidacris cristata*) and royal ground snake (*Liophis reginae*) are likely to suffer range loss due to increase temperature (Diniz-Filho et al. 2010; Mesquita et al. 2013). Anticipating the effects of future climate change on species distributions should be a conservation priority (Raxworthy et al. 2008).

In response to climate change, species may adapt, disperse or become extinct (Berg et al. 2010). How species will respond to climate variations will depend on their environmental tolerance, dispersal abilities and biological interactions (Soberón and Peterson 2005; Soberón 2007; Peterson et al. 2011). Species that are sensitive to climate and limited by dispersal may be unable to adapt to novel climates or to disperse to new suitable regions (Foden et al. 2008; Bellard et al. 2012), and many calls for so-called assisted migration have been put forth (McLachlan et al. 2007). Populations will only be viable over the long-term if future climate that is appropriate is found in regions into which the organisms can easily disperse (climatic refuges) and understanding future climate and dispersal ability should also be a conservation priority.

Because of climate change, potential refuges may not be geographically stable (Wiens et al. 2011). Thus, if we wish to maintain species, protected areas for climate refuges should be determined based on both present and future conditions and have the potential to change over time (Griffith et al.

2009; Cole and Yung 2010). In Brazil, as in most countries, national parks and conservation areas do not fulfill these requirements in the present and are unlikely to in the future, and, as a consequence, many species needing protection will not be found within any conservation units that can provide that protection (Oliveira et al. 2017).

Amphibians are very sensitive to climate variation for several reasons, including dispersal, physiological and reproductive limitations, among others (Duellman and Trueb 1994; Foden et al. 2008; Ochoa-Ochoa et al. 2012). Approximately one third of all species of amphibians in the world are threatened with extinction, 52% of which are susceptible to climate change, and so amphibians are among the most threatened groups of animals (Stuart et al. 2004; Foden et al. 2008; Hof et al. 2011). The consequences of climate change for amphibians vary. For example, / of diversity for Chinese amphibians will be accompanied by loss of 20% of their original ranges (Duan et al. 2016). In South America, a contraction of the distribution is predicted for some species of *Dendropsophus* in Brazil (Vasconcelos and Nascimento 2015), while expansion of the distributions of the invasive bullfrog *Lithobates catesbeianus* is also predicted in Brazilian Atlantic Forests (Loyola et al. 2014). Also, increasing temperature may reach 9˚C warmer than today, accompanied by a decrease in rainfall in northeastern Brazil (Chou et al. 2014), thus dramatically changing the climate regime for many dispersal limited species.

The frog genus *Phyllodytes* (Anura, Hylidae) comprises 17 species endemic to coastal eastern Brazil. Frogs were mostly found in lowlands (less than 1000 m), in open areas of sandy coastal plains and rocky outcrops (rather than forest *sensu strictu*, but within the ecoregion of the Atlantic Forest) many of which are isolated. The genus *Phyllodytes* arose along with an obligate relationship with tank bromeliads, where they live and reproduce (Peixoto 1995; Haddad and Prado 2005). This old association allows them to inhabit regions in which the more arid climate may be considered marginal or uninhabitable for most frog species. *Phyllodytes* survive aridity because of their association with bromeliads and how that association, along with climate, influences the future distribution of these frogs is the subject of this study. Here, we use ecological niche models (ENMs) to: 1) predict the effects of future climate change on the distribution of the genus *Phyllodytes*, 2) Predict which of the several species of *Phyllodytes* are likely to go extinct before the end of the century, and 3) identify potentially climatically stable areas within the range of the genus that may be essential for the conservation and persistence of *Phyllodytes*.

MATERIALS AND METHODS

Phyllodytes occurrence records were obtained from Mageski et al. (2018) using Species Link (CRIA 2016), Global Biodiversity Information Facility (GBIF 2016), relevant literature and field observations from 2007 to 2015 in the state of Espírito Santo, Brazil. In the field, vocalizing frogs were located by their calls and additional frogs were found by searching appropriate tank bromeliads (Rödel and Ernst 2003; Mageski et al. 2015). ArcGIS 10 (ESRI 2011; Kozak et al. 2008) was used to construct maps. Here, we assume that because bromeliads used by *Phyllodytes* are widespread throughout most of South America, they are not limiting and so need not be included in modeling.

Environmental layers

Bioclimatic data are from Ecoclimate with resolution of 0.5° (Lima-Ribeiro et al. 2015). We chose variables first that were relatively independent among each other (to avoid multicollinearity, $r < 0.7$) and that are biological meaningful to the frogs following Mageski et al. (2008): isothermality (Bio 3), maximum temperature of warmest month (Bio 5), minimum temperature of coldest month (Bio 6), annual range in temperature (Bio 7), annual precipitation (Bio 12), precipitation seasonality (Bio 15) and precipitation of driest quarter (Bio 17). We modeled two scenarios that are predictions of the minimal and maximal temperature increases expected by the end of the century: 1) minimum will increase by 0.3°-1.7°C and 2) maximum will increase by 2.6°-4.8°C (IPCC 2014). We will see that despite the relatively small differences between these two extremes, the consequences are large.

We used bathymetry and orography models for South America from ETOPO1 Bedrock (available at: https://www.ngdc.noaa.gov) and predictions by the Intergovernmental Panel on Climate Change (IPCC 2014) to identify sea level variation under different models of greenhouse gas emissions, using the package raster (Hijmans et al. 2016a) in R 3.3.0 (R Development Core Team 2016). Subsequently, we converted rasters to polygons and masked climatic layers, eliminated ocean cells and estimated future sea level. Finally, we cropped all raster layers to South America (-100º to -30º longitude, -60º to 30º latitude) as a landscape, using the package raster.

Protected areas

Polygons (shapefiles) of Brazilian protected areas were obtained from the Brazilian Environment Ministry (BEM 2017) and which include national and state parks, ecological field stations and any kind of reserve in which some kind of environmental protection is provided. We converted the layers from their original SAD 1969 projection to a geographic latlong WGS84 projection, to match the environmental variables, in ArcGIS 10 (ESRI 2011).

Species distribution models

We used the model in Mageski et al. (2018), adjusted with 75% of the data for training and 25% for testing, in 1000 iterations and beta multiplier of 2 and data from IPCC (2014) to predict suitable areas in the future. All models used the extent of South America (-30º to -90º longitude, -60º to 15º latitude) as landscape. Here, because the bromeliad species used by *Phyllodytes* are widespread throughout most of South America, we assume they are not limiting and so need not be included in modeling. To quantify the changes in suitable climate area for frogs in present and future, we reclassified the predictive maps into binary maps using threshold that maximizes sensitivity and specificity that minimize omission and comission errors, and calculated the area of predictive range (km²) using raster package in R. Binary (presence – absence) maps are used to put current and future potential distribution of *Phyllodytes* in the context of protected areas available in eastern Brazilian coast. We used polygons of the protected areas as a mask for the current and future potential binary distribution, and calculated area (km^2) and percentage of the prediction within protected areas.

RESULTS

The current distribution of *Phyllodytes* is already limited in habitat subsets of the Atlantic Forest of eastern Brazil (Fig. 1). Our models predicted a reduction in the distribution of *Phyllodytes* within a very fragmented region within which it is currently found in eastern Brazil (Fig. 2A-C). Models indicate that in the northern part of the current range (Fig. 2A) the climatically suitable area will be dramatically reduced in the minimal change scenario (Fig. 2B) while it will disappear completely under the maximum change scenario, with extinction of all species currently found in that region (11 species, 65% of all species in the genus, Figs. 2C, 3A). The future distribution is predicted to decrease by nearly 80% and will be limited to the states of Espírito Santo and Rio de Janeiro (Fig. 2C) and the probability of persistence will vary from 73% (Fig. 2B) to 25% (Fig. 2C).

Currently, only 35% of *Phyllodytes* records were in protected areas and those were in a mere 20 of the 215 areas (Table 1; Fig. 2D). Our models suggested that the climate suitable for the frogs comprises 560,000 km^2, of which only 170,000km^2 (30%) are wholly or partially within protected areas. As temperatures increase, the number of protected areas with climate suitable for *Phyllodytes* will decrease from 215 to 188 (Fig. 2E; Table 1). Also, this will result in a loss of 3,440 km^2 (2%) of the area being protected. With maximal temperature increase, half of the protected areas will vanish (Fig. 2F; Table 1), with a loss of 96,000 km^2 (56%). Only the states of Espírito Santo and Rio de Janeiro (only the northern region near the border with Espírito Santo; Fig. 2A-C) will maintain regions with climate hospitable for *Phyllodytes*. With minimal temperature increase, the protected areas with appropriate climate will be the same as those currently in existence (49,295 km^2 or 59% in 26 protected areas in Espírito Santo, 29,000 km^2 or 78% in 51 protected areas in Rio de Janeiro; Table 1, Figs. 2B, 2E). With maximal temperature increase the suitable area will decrease from 49,300 to 46,400 km^2, a decline of 6%, with 62% of these areas being protected today in Espírito Santo, and from the current 29,000 to 26,000, a decline of 10%, with 77% being protected in Rio de Janeiro (Table 1; Fig. 2C; and Fig. 2F).

DISCUSSION

Due to increasing temperatures, several species in the genus *Phyllodytes* are likely to be extinct by the end of the century, and the remaining species will be at risk, with fragmented populations among increasingly fragmented habitat. All populations in the northern half of the current distribution of the genus will be lost if temperatures increase ca. 5ºC, and some predictions suggest that in that region the temperature will increase by 9ºC (Chou et al. 2014). Similar loss of areas with suitable climate were predicted for mammals in northern South American (Schloss et al. 2012). The combination of increasing temperature and decreasing rainfall will drastically change the regional climate, more so than other regions of Brazil (Marengo et al. 2009; Chou et al. 2014; Lemes et al. 2014). Thus, conservation of this genus, and probably other groups of amphibians as well (Loyola et al. 2013) should become a priority and perhaps the genus, or at least several of the poorly known species, should be considered endangered today. Studies have suggested that to compensate for climate change, species will have to move to higher elevations or away from the equator to remain in climatically appropriate regions (Peterson and Vose 1997). These options do not exist for *Phyllodytes* due to dispersal limitation, habitat fragmentation and the possibility of changing biological interactions that may become important in the changing climate (Mageski et al. 2018).The fraction of the distribution of *Phyllodytes* that is within protected areas is also likely to decrease over time and increasing temperatures. Also, there is no guarantee that the currently available protected areas will continue to be suitable as temperatures rise (Griffith et al. 2009). For example, it is predicted that 1,412 km^2 of area with suitable climate for Californian birds will disappear in less than 90 years (Wiens et al. 2011). In southeastern Brazil, increasing temperature and sea levels will make coastal regions uninhabitable for many lowland amphibians (Lemes et al. 2014; Soares de Oliveira et al. 2016).

Climate suitable for *Phyllodytes* will only remain in the states of Espírito Santo and Rio de Janeiro, more or less in the same regions occupied today. A small Atlantic Forest refuge was predicted at the boundaries of Espírito Santo and Rio de Janeiro during the last glacial maximum (ca. 21,000 years ago; Carnaval et al. 2009). This region has apparently been stable for *Phyllodytes* since the Pliocene (3 mya, 21 kya and 6 kya, Mageski et al. 2018). Because this will be the only region with suitable climate for *Phyllodytes*, we suggest that conservation efforts be directed to discovering and maintaining populations here. In addition, only introduced populations of *Phyllodytes* (*P. luteolus*) are found anywhere farther south than northern Rio de Janeiro and which were probably carried accidentally in ornamental bromeliads (Salles and Silva-Soares 2010; Forti et al. 2017). Nothing is known about these individual populations. But, these two introduced populations are within the region that will continue to be adequate for *Phyllodytes* (Mageski et al. 2018). Consequently, the state of Espírito Santo is currently the southernmost natural limit of *Phyllodytes* (Schineider and Teixeira 2001; Ferreira et al. 2012; Haddad et al. 2013; Mageski et al. 2015; 2016; Motta-Tavares et al. 2016; Frost et al. 2017).

With these results in mind, we suggest an increase of number of protected areas in state of Espírito Santo, especially in coastal regions, in which several amphibians species are also threatened by extinction with increasing temperature and, consequently sea level, that vary from 1 to 6 m by the end of the century (Overpeck et al. 2006; Grinsted et al. 2010; Nicholls and Cazenave 2010, IPCC 2014). Those new protected areas, similar to those with *Phyllodytes* (e.g. climatically suitable, with appropriate bromeliads and few potential competitors, Mageski et al. 2018), must be implemented as corridors that connect with those protected areas that already exist to remain viable and stable populations of *Phyllodytes* in the future. Finally, it will be also important to document the potential turnover of the local amphibian communities, identify the climatic shifting points, and document which new species (or populations) are found (and if) they can adapt to ongoing climate changes.

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Table 1. Protected areas inside *Phyllodytes* current prediction. States are Alagoas (AL), Bahia (BA), Espírito Santo (ES), Minas Gerais (MG), Paraíba (PB), Pernambuco (PE), Paraná (PR), Rio de Janeiro (RJ), Rio Grande do Norte (RN), Santa Catarina (SC), Sergipe (SE), and São Paulo (SP). Protected area unsuitable under minimal temperature increase (1) and maximal temperature increase (2).

Name	State
Adjacent areas of the Parque Estadual do Ri[1,2]	MG
Anhatomirim	SC
Araras[1,2]	RJ
Arqueológica de Guaratiba	RJ
Arquipélago das Três Ilhas	ES
Augusto Ruschi	ES
Bacia do Cobre S. Bartolomeu[2]	BA
Bacia do Frade	RJ
Bacia do Rio Macacu	RJ
Bacia do Rio São João/Mico-Leão-Dourado	RJ
Baía de Camamu[2]	BA
Baía de Todos os Santos[2]	BA
Baleia Franca	SC
Barra do Rio Mamanguape[1,2]	PB
Boguaçu	PR
Cachoeira da Fumaça	ES
Cairuçu[2]	RJ
Caminhos Ecológicos da Boa Esperança[2]	BA
Cananéia-Iguape-Peruíbe	SP
Canavieiras[1,2]	BA
Caparaó	ES-MG
Caraguatá	SC
Caraíva/Trancoso[2]	BA
Carbocloro[2]	SP
Carijós	SC

Carlos Botelho[2]	SP
Catimbau[2]	PE
Centro Ecológico Metodista Ana Gonzaga	RJ
Chaúas	SP
Conceição da Barra	ES
Coroa Vermelha[2]	BA
Corobobó[1,2]	BA
Córrego do Veado	ES
Córrego Grande	ES
Costa de Itacaré/Serra Grande[2]	BA
Costa dos Corais[2]	AL-PE
Descobrimento[2]	BA
Desengano	RJ
Duas Bocas	ES
Ecoparque de Una[2]	BA
El Nagual[1,2]	RJ
Estação Vera Cruz[2]	BA
Fazenda Agro-Pastoril Gonçalves[2]	SP
Fazenda Águia Branca[2]	BA
Fazenda Araçari[2]	BA
Fazenda Arco-Íris	RJ
Fazenda Avaí[2]	BA
Fazenda Bom Retiro	RJ
Fazenda Bom Sossego	BA
Fazenda Cachoeirinha	RJ
Fazenda Cafundó	ES
Fazenda Califórnia	MG
Fazenda Coqueiros[2]	BA
Fazenda Córrego da Luz	RJ
Fazenda Flor de Liz[2]	BA
Fazenda Itacira	BA
Fazenda Kaybi[2]	BA
Fazenda Limeira[1,2]	RJ

Fazenda Lontra/ Saudade[1,2]	BA
Fazenda Mato Grosso	RJ
Fazenda Meandros[2]	SP
Fazenda Paraíso[2]	BA
Fazenda Pedra de Água[1,2]	PB
Fazenda Pindorama[2]	BA
Fazenda Roça Grande	RJ
Fazenda Santa Beatriz do Carnijó[1,2]	PE
Fazenda Santa Cristina	ES
Fazenda São João[2]	BA
Fazenda Várzea[1,2]	PB
Floresta do Jacarandá[1,2]	RJ
Fonte da Bica[2]	SE
Fonte Grande	ES
Forno Grande	ES
Gleba o Saquinho de Itapirapuã[2]	RJ
Goytacazes	ES
Graciosa	PR
Granja Redenção	RJ
Guanandy	ES
Guapi-Mirim	RJ
Guaraguaçu	PR
Guaraqueçaba	PR
Guaratuba	PR
Guaribas[1,2]	PB
Guaxindiba	RJ
Histórico do Monte Pascoal[2]	BA
Ilha Comprida	SP
Ilha das Flores	ES
Ilha do Ameixal[2]	SP
Ilha do Cardoso	SP
Ilha do Mel[2]	PR
Ilhas de Tinharé e Boipeba[2]	BA

Itapeti[2]	SP
Itaúnas	ES
Jacarenema	ES
Jacarepiá	RJ
Jacupiranga	SP
Joanes Ipitanga[2]	BA
Joatinga[2]	RJ
Juréia-Itatins[2]	SP
Jurupará[2]	SP
Lago de Pedra do Cavalo[2]	BA
Lagoa do Peixe[2]	BA
Lagoa Encatada e Rio Almada	BA
Lagoas de Guarajuba[2]	BA
Lagoas e Dunas do Abaeté[2]	BA
Lazer de Parati-Mirim[2]	RJ
Litoral Norte do Estado da Bahia[2]	BA
Macaé de Cima	RJ
Mandira	SP
Mangaratiba	RJ
Maria Francisca Guimarães[1,2]	RJ
Maricá	RJ
Marinha Arraial do Cabo	RJ
Marinha de Pirajubaé	SC
Marinha do Corumbau[2]	BA
Marinha Lagoa do Jequiá[2]	AL
Marinho dos Abrolhos[2]	BA
Mário Xavier	RJ
Marituba do Peixe[2]	AL
Massambaba	RJ
Mata das Flores	ES
Mata do Iguatemi[2]	SP
Mata do Pau Ferro[1,2]	PB
Mata do Sossego[1,2]	MG

Menino Deus	SC
Mestre Álvaro	ES
Morro do Curussu Mirim[2]	SP
Murici[2]	AL
Nascentes do Tietê	SP
Nísia Floresta[1,2]	RN
Normano Tedesco	SC
Nossa Senhora do Oiteiro de Maracaípe[1,2]	PE
Onças[1,2]	PB
Pacotuba	ES
Palmito	PR
Panema[2]	BA
Paraíso	RJ
Pariquera abaixo	SP
Parque e Fazenda do Carmo[2]	SP
Pau Brasil in Bahia[2]	BA
Pau Brasil in Rio de Janeiro	RJ
Pau-Oco	PR
Pedra Azul	ES
Pedra Branca	RJ
Pedra dos Amarilis[1,2]	RJ
Pedra Talhada[2]	AL-PE
Petrópolis[1,2]	RJ
Piaçabuçú[2]	AL
Pico do Goiapaba-Açu	ES
Pico Marumbi[2]	PR
Plataforma Continental do Litoral Norte[2]	BA
Poço das Antas	RJ
Ponta da Baleia/Abrolhos[2]	BA
Pontões Capixabas	ES
Praia Mole	ES
Pratagy[2]	AL
Pratigi[2]	BA

Raso da Catarina[1,2]	BA
Reserva Ecológica Sebuí	PR
Reserva Fugidos[2]	BA
Restinga de Jurubatiba	RJ
Rio Capivara[2]	BA
Rio da Onça	PR
Rio Doce[1,2]	MG
Rio Pequeno	PR
Rio Piraquara	PR
Rio Preto	ES
Saint-Hilaire/Lange	PR
Saltinho[2]	PE
Santo Antônio[2]	BA
Sapiatiba	RJ
Serra Branca/Raso da Catarina[1,2]	BA
Serra da Baitaca[2]	PR
Serra da Bocaina[2]	SP-RJ
Serra da Tiririca	RJ
Serra de Itabaiana[2]	SE
Serra do Conduru[2]	BA
Serra do Mar – Núcleo Caraguatatuba	SP
Serra do Mar – Núcleo Cunha-Indaiá[2]	SP
Serra do Mar – Núcleo Curucutu[2]	SP
Serra do Mar – Núcleo Cutatão	SP
Serra do Mar – Núcleo Pedro de Toledo[2]	SP
Serra do Mar – Núcleo Picinguaba[2]	SP
Serra do Mar – Núcleo Santa Virgínia[2]	SP
Serra do Mar – Núcleo São Sebastião	SP
Serra do Mar in Paraná	PR
Serra do Mar in São Paulo[2]	SP
Serra do Tabuleiro	SC
Serra do Teimoso[2]	BA
Serra dos Orgãos[1,2]	RJ

Serras do Gericinó-Mendanha	RJ
Sete Salões	MG
Sítio Cachoeira Grande	RJ
Sítio Granja São Jorge	RJ
Sítio Poranga	RJ
Sítio Santa Cruz	RJ
Sítio São Domingos/Agartha	MG
Sítio Shangrilah	RJ
Sooretama	ES
Superagui	PR
Tamoios[2]	RJ
Tietê[1,2]	SP
Tinguá	RJ
Toque Toque Pequeno	SP
Três Picos	RJ
Tupinambás[1,2]	SP
Tupiniquins[2]	SP
Una[2]	BA
União	RJ
Várzea do Rio Tietê	SP
Vera Cruz[2]	AL
Wenceslau Guimarães[2]	BA
Xixová-Japuí[2]	SP
Xituê[2]	SP

Figure captions

Fig. 1.— Geographical distribution of the bromeliad frog genus *Phyllodytes* South America. Abbreviations for the states are Alagoas (AL), Bahia (BA), Espírito Santo (ES), Minas Gerais (MG), Paraíba (PB), Pernambuco (PE), Paraná (PR), Rio de Janeiro (RJ), Sergipe (SE), and São Paulo (SP).

Fig. 2.— Climate suitability for bromeliad frog genus *Phyllodytes* from current (A) to the 2080-2100, under minimal increase 0.3°-1.7°, B) and maximal increase 2.6°-4.8°C, C) scenarios. Models results according Mageski et al. (2018): AUC = 0.99 (in both, in training and testing), TSS = 0.97. The three most important variables (as measured by permutation importance, PI) in this model were annual range in temperature (PI = 34.2), isothermality (30.1) and precipitation of the driest quarter (17.2).

Fig. 3.— Binary predictions for bromeliad frog genus *Phyllodytes* and available protected areas from current (A) to the 2080-2100, under minimal increase 0.3°-1.7°, B) and maximal increase 2.6°-4.8°C, C) scenarios.

Figure 1


N
Brazil
PB
PE
AL
SE
BA
MG
ES
SP
RJ
Atlantic ocean
Phyllodytes
Atlantic Forest
0
400
800 km

Figure 2

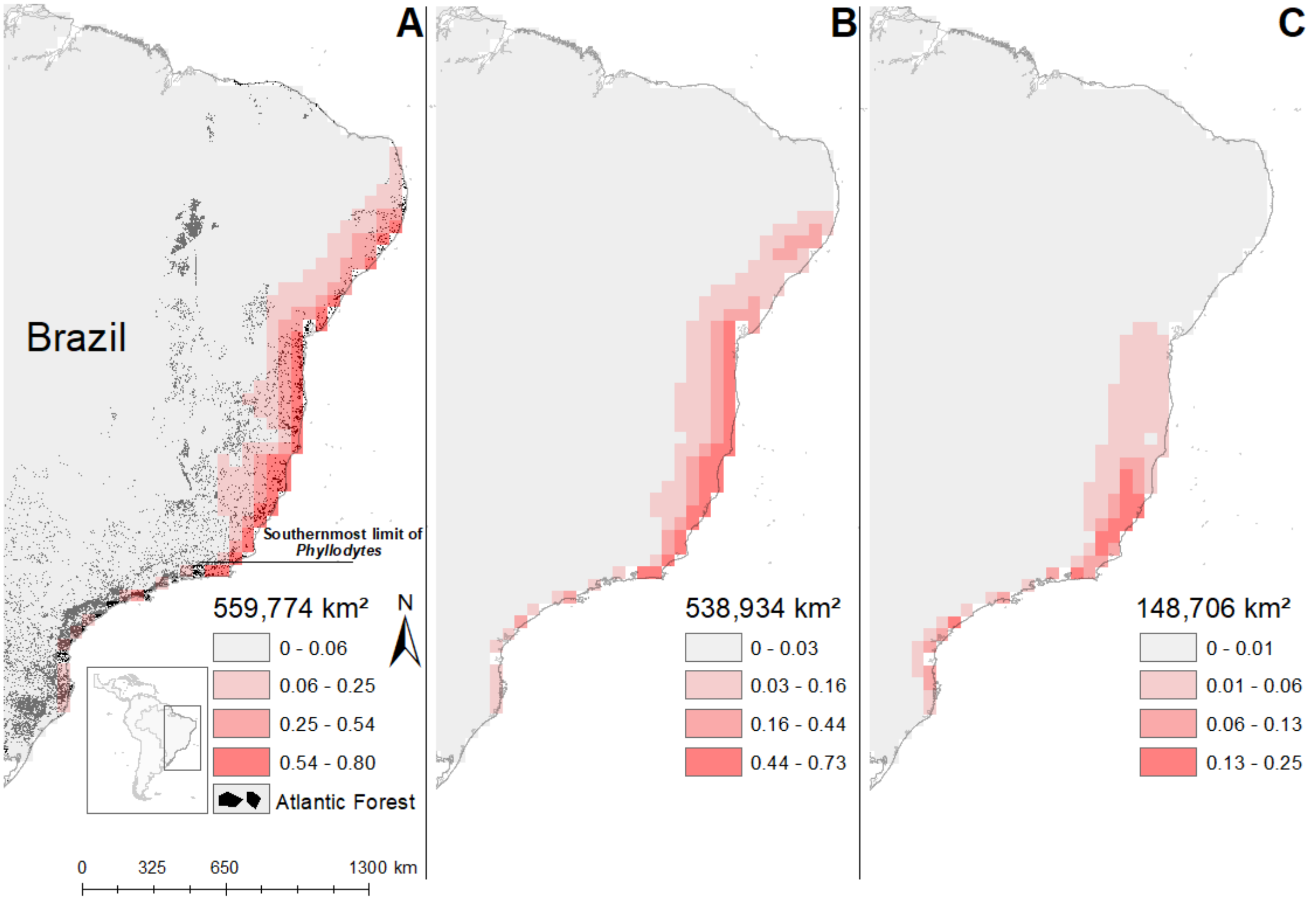
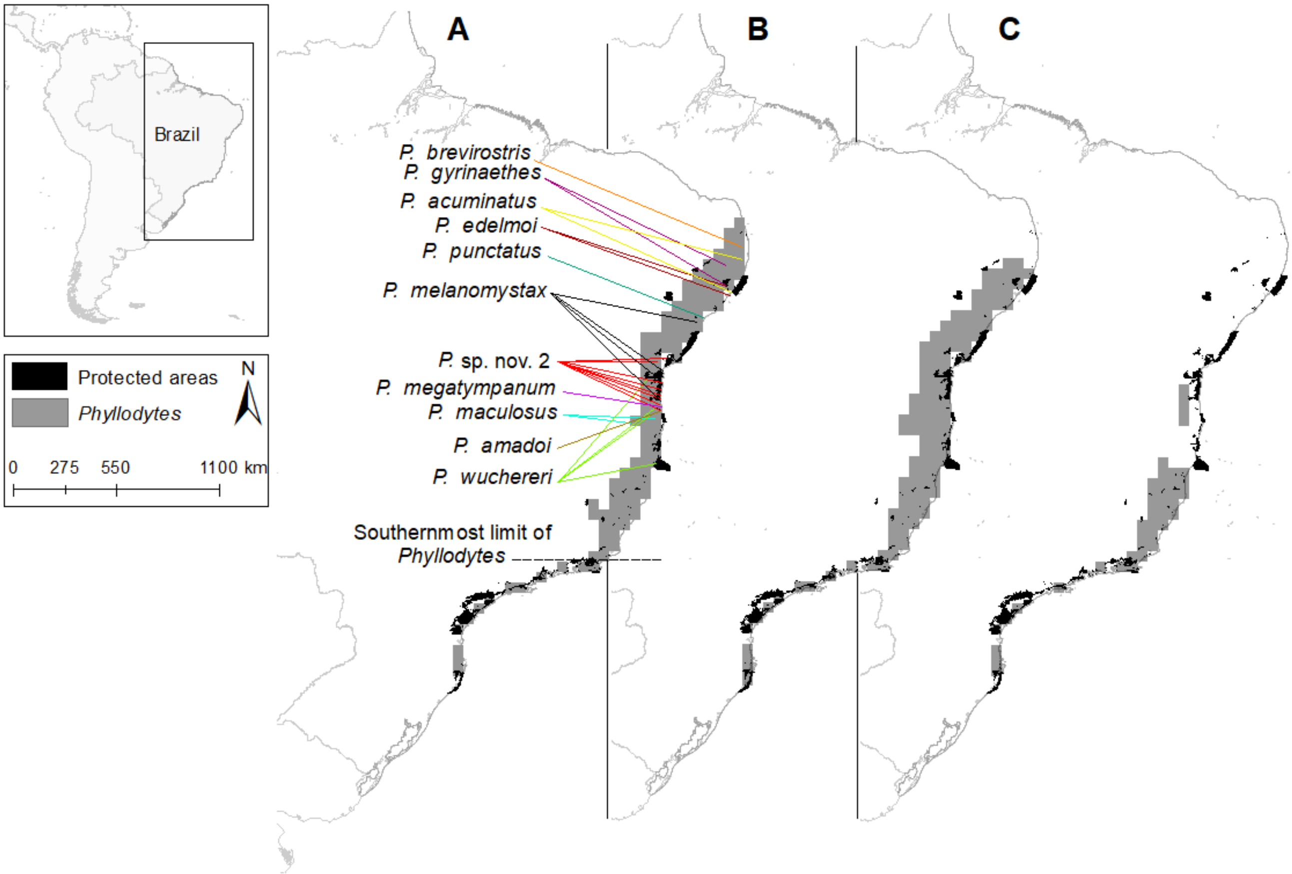

A
B
C
Brazil
Southernmost limit of *Phyllodytes*
559,774 km²
0 - 0.06
0.06 - 0.25
0.25 - 0.54
0.54 - 0.80
Atlantic Forest
N
0
325
650
1300 km
538,934 km²
0 - 0.03
0.03 - 0.16
0.16 - 0.44
0.44 - 0.73
148,706 km²
0 - 0.01
0.01 - 0.06
0.06 - 0.13
0.13 - 0.25

Figure 3


Brazil
Protected areas
Phyllodytes
N
0 275 550 1100 km
A
B
C
P. brevirostris
P. gyrinaethes
P. acuminatus
P. edelmoi
P. punctatus
P. melanomystax
P. sp. nov. 2
P. megatympanum
P. maculosus
P. amadoi
P. wuchereri
Southernmost limit of
Phyllodytes

CONCLUSÕES GERAIS

Embora as evidências tenham sugerido que *Phyllodytes* surgiu na Amazônia, todas as espécies estão atualmente isoladas na costa leste da Mata Atlântica, em áreas com bromélias e climaticamente diferentes daquelas ao entorno. Apesar da atual distribuição ser restrita, os modelos mostraram que os sapos poderiam ter tido uma distribuição mais ampla (principalmente pelos limites unilaterais), uma vez que sempre tinha clima adequado e bromélias. Mas, *Phyllodytes* mostrou aparente limitação de distribuição em áreas com maior riqueza de outros sapos, potenciais predadores e competidores. Assim, essa interação com outras espécies relegou *Phyllodytes* a habitar áreas com condições climáticas marginais (mais quentes e secas), o que provavelmente é possível graças ao uso das bromélias. Embora essas áreas as quais *Phyllodytes* ocupa atualmente aparentemente mantém as populações viáveis, no futuro serão um tanto complicadas. Com o crescente aumento de temperatura e, consequentemente, do nível do mar, a distribuição de *Phyllodytes* foi prevista apenas para os estados do Espírito Santo e Rio de Janeiro (cenário pessimista), ainda com baixa adequabilidade. Assim, baseados 1) na restrita distribuição de *Phyllodytes* (principalmente para as espécies as quais são conhecidas poucos registros), 2) na limitação imposta pelas interações (bromélias e outros sapos) 3) na intensa fragmentação da Mata Atlântica e 4) na redução de clima potencial no futuro (tanto na área, quanto na adequabilidade), concluimos que todas as espécie do gênero estão ameaçadas por extinção em um curto período de tempo (menos que 100 anos). Assim, recomentamos a revisão do estatus de conservação frente à “International Union for Conservation of Nature (IUCN)” e que medidas eficazes (como a implantação de corredores entre os fragmentos de Mata Atlântica adequados) sejam urgentemente tomadas objetivando a conservação do gênero.