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Taxonomia, biogeografia e conservação dos anfíbios da Serra do Espinhaço

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Taxonomy, biogeography and conservation of anurans in the Espinhaço Range, Brazil

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Introdução Geral

Os anfíbios modernos são possivelmente o grupo existente de vertebrados terrestre mais antigo, existindo desde o Médio Permiano (± 305 - 290 m.a.; Alford et al., 2007; Marjanovic & Laurin, 2007; Pyron and Wiens, 2011). Apesar disso, apenas recentemente se atentou para sua grande diversidade de espécies, sendo este o grupo de vertebrados terrestres que teve o maior número de espécies descritas nas últimas décadas (Köhler et al., 2005). Atualmente são conhecidas cerca de 6890 espécies (AmphibiaWeb, 2012), sendo que a melhor estimativa para o número total de espécies é de 8000–12000 (Parra, 2005). O grupo possui um importante papel na dinâmica dos nutrientes, promovendo o fluxo de energia entre os sistemas terrestres e aquáticos (Alford et al., 2007).

Anfíbios também constituem o grupo de vertebrados terrestre mais ameaçado do mundo: pelo menos 37% estão classificados como vulneráveis, em perigo ou criticamente ameaçados (IUCN, 2012). Esta situação é certamente otimista visto que 25% possuem status de conservação desconhecido (IUCN, 2012). Declínios populacionais detectados em todo o mundo têm gerado uma crescente preocupação em relação à conservação desse grupo (Stuart et al. 2004, Hoffmann et al. 2010). As causas desses declínios são assunto de pesquisa contínua, mas provavelmente incluem modificações no uso do solo, mudanças climáticas e a proliferação da doença quitridiomicose causada por um fungo patogênico (Stuart et al., 2004; Blaustein & Kiesecker, 2002; Beebee & Griffiths, 2005). Infelizmente, o panorama futuro tende a ser muito pior em 2080 (Hof et al., 2011), visto que as áreas que abrigam as faunas mais ricas de anfíbios serão desproporcionalmente mais afetadas por um ou múltiplos fatores de ameaça (doenças e mudanças climáticas ou no uso do solo) do que áreas de baixa riqueza. Dada a seriedade das ameaças atuais aos anfíbios, é crucial o desenvolvimento de planos para proteger sua diversidade. Para tal, a necessidade de dados de taxonomia e distribuição geográfica de alta qualidade, dos quais derivam estudos científicos confiáveis, é bastante obvia.

O Brasil abriga a maior riqueza de anfíbios do mundo (IUCN, 2012). Atualmente, 946 espécies são conhecidas para o país (Segalla et al., 2012). Contudo, para manejar tamanha diversidade, frente às crescentes ameaças, precisamos saber quais são as unidades taxonômicas básicas que a compõe, onde ela está, como se encontra organizada em diferentes escalas, como as suas diferentes facetas covariam no espaço e no tempo e como respondem a um conjunto desconcertante de variáveis que atuam e interagem, mediando a diversidade e a distribuição das espécies por meio de inúmeros mecanismos e processos. Entretanto, o conhecimento acerca da biodiversidade permanece inadequado, visto que a maioria das espécies do planeta ainda não foi formalmente descrita (‘the Linnean shortfall’) e a distribuição geográfica da maioria das espécies é superficialmente conhecida (‘the Wallacean shortfall’, Whittaker et al., 2005). Essa carência de informação é especialmente grave em regiões tropicais (Kress et al., 1998; Bini et al., 2006), principalmente em regiões montanhosas onde muitos gêneros e espécies de vertebrados ainda estão sendo descritas ano após ano (e.g. Rodrigues et al., 2009; Percequillo et al., 2011) e os registros individuais são consideravelmente espaçados e/ou enviesados espacialmente devido a seu isolamento e difícil acesso.

A maior cadeia de montanhas da América do Sul fora os Andes, a Serra do Espinhaço, não é exceção à regra e é caracterizada, ao mesmo tempo, por uma biota única e extremamente rica (Giulietti et al., 1997) e por enormes lacunas do conhecimento no que se refere a diversos taxa (Versieux & Wendt, 2007; Echternacht, 2011), incluindo os anfíbios (Leite et al., 2008). Localizada entre dois hotspots globais de biodiversidade (i.e. a Mata Atlantica e o Cerrado) e ainda inserida em um bioma semi-arido (i.e. Caatinga), o Espinhaço estende-se latitudinalmente por cerca de 1000 km, cortando os estados de Minas Gerais e Bahia. A complexidade de suas relações (ecológicas e históricas) com os demaias domínios morfoclimáticos brasileiros, aliada a sua grande heterogeneidade ambiental, propiciou condições diversas para o estabelecimento de uma grande variedade de fitofisionomias (e.g. campos rupestres, matas de galeria, matas nebulares, cerrados, veredas). O conjunto dessas caracteristicas faz com que a região seja consistentemente apontada como área prioritária para a conservação do Brasil (MMA, 1999, 2000a, 2000b, 2003) e do estado de Minas Gerais (Drummond et al., 2005). Devido ao seu relevo acidentado, as terras altas do Espinhaço permaneceram menos alteradas do que os vales de baixada e encostas a elas adjacentes, oferecendo uma única possibilidade de se conservar parte do que ainda resta da biodiversidade original desses três ameaçados domínios fitogeográficos brasileiros. Apesar disso, o elevado número de espécies ameaçadas de distribuição restrita (MMA, 2008; IUCN, 2012) e as crescentes taxas de descaracterização de habitats causadas pela ação antrópica (Safford, 1999; Jacobi et al., 2007; Versieux & Wendt, 2007; Barbosa et al., 2010) salientam a necessidade urgente de ações de conservação. Apesar de sua relevância para a conservação da biodiversidade brasileira, uma pequena parcela da área da Serra do Espinhaço encontra-se protegida em reservas (Silva et al., 2008).

Ao mesmo tempo em que o difícil acesso permitiu que algumas áreas do Espinhaço se mantivessem preservadas, ele também dificultou que grandes coletas de anfíbios (e outros táxons) fossem feitas na região. Ressalvas devem ser feitas aquelas realizadas por Werner Bokermann e Ivan Sazima durante as décadas de 1960 e 1970, quando a maior parte das espécies endêmicas da porção sul do Espinhaço foram identificadas e/ou descritas. Muitas das localidades mais interessantes da Serra do

Espinhaço só podem ser acessadas a pé e, portanto, permaneceram inexploradas por muito tempo. Como exemplo da nossa ignorância, das 47 espécies de anfíbios identificadas nesse estudo como endêmicas, 13 ainda não foram descritas, apesar de serem facilmente diagnosticáveis. Apesar da proximidade da sua porção meridional (Quadrilátero Ferrífero e Serra do Cipó) com a metrópole de Belo Horizonte, que concentra a maior parte dos taxonomistas do estado de Minas Gerais, muitas espécies da região são ainda frequentemente identificadas de maneira errônea, o que pôde ser claramente observado nos acervos das coleções visitadas durante o presente estudo. Além de terem distribuição geográfica restrita, algumas vezes conhecida de uma ou poucas localidades, muitas espécies possuem hábitos crípticos e reprodução explosiva, fatores que dificultam ainda mais seu encontro e coleta. Ainda, o pequeno número de taxonomistas em relação ao número de espécies a ser estudada e a falta de apoio institucional e de órgãos de fomento a este tipo de pesquisa básica, muitas vezes taxada de pouco relevante, fortalece ainda mais o desconhecimento sobre esse peculiar grupo de vertebrado. Contudo, tal panorama vem mudando, sendo que oito espécies endêmicas do Espinhaço foram descritas nos últimos cinco anos (Cassimiro et al., 2008; Caramaschi et al., 2009; Lourenço et al., 2009; Cassini et al., 2010, Maciel & Nunes, 2010; Leite et al., 2011; Napoli et al., 2011; Leite et al., 2012), a maioria delas fruto do trabalho de novos taxonomistas. Entretanto, como observado por Leite et al. (2012), muitas espécies ainda aguardam descrições formais (e.g. Carvalho et al., in prep.; Barata et al., in prep.).

Taxonomia e conservação de espécies são frequentemente assumidas como atividades interdependentes. Contudo, a taxonomia está subjacente e intrinsicamente ligada à preservação da diversidade biológica. Não podemos almejar a conservação de organismos que não podem ser identificados, e as nossas tentativas para entender as consequências das modificações e degradação ambientais estarão fatalmente comprometidas caso não formos capazes de reconhecer e descrever os integrantes dos sistemas naturais. Portanto, tanto a carência de conhecimento e habilidade taxonômica, quanto confusões sobre onde o ‘limite’ de uma espécie deve ser definido, causam problemas para os conservacionistas. Contudo, taxonomia e conservação definitivamente não são a mesma coisa. Descrever espécies e suas relações não é garantia de sua conservação. Lista de espécies completas ou revisões taxonômicas por si só são ineficientes do ponto de vista da conservação. Entretanto, seria impossível desenvolver estratégias e mecanismos necessários para a conservação de espécies na ausência do conhecimento adequado sobre a distribuição e a taxonomia das mesmas. Como herpetólogo e conservacionista, acredito que diminuir a distância entre taxonomistas e conservacionistas é um ponto crítico, e cada um de nós deveria se sentir insentivado a tomar parte desta tarefa, tornando-se pessoalmente mais proficiente em taxonomia e história natural de maneira a encurtar este hiato.

Esta tese está dividida em quatro capítulos, escritos em inglês, na forma de artigos para publicação em revistas internacionais. Todas as questões abordadas estão intimamente ligadas à disciplina da biogeografia da conservação, que foi formalmente definida por Whittaker et al. (2005), como a “aplicação dos princípios, teorias e análises biogeográficas aos problemas relativos à conservação da biodiversidade”. O primeiro capítulo traz uma descrição detalhada do sistema de estudo, apresentando uma lista de espécies atualizada à luz de uma detalhada revisão de museu e de um grande esforço de campo. Beneficiando de modelos de distribuição de espécies, descrevo nele os padrões espaciais de riqueza de espécies e endemismo, considerando toda a extensão do Espinhaço, de maneira a possibilitar uma avaliação da eficiência do atual sistema de unidades de conservação em conservar as suas 47 espécies endêmicas. Este capítulo encontra-se em fase final de preparação e será submetido ao periódico *Conservation Biology*. No segundo capítulo identifico as áreas de endemismo de anuros da cadeia, exploro as suas relações e avalio a influência do clima atual e pretérito, desde o último máximo glacial, na configuração e distribuição dessas áreas. Pretende-se submeter este capítulo ao periódico *Journal of Biogeography*. No terceiro e quarto capítulos apresento as descrições, recentemente publicadas no periódico *Herpetologica*, de duas espécies novas de distribuição muito pequena e restrita a duas áreas de endemismo identificadas no segundo capítulo, uma em Minas Gerais e outra na Bahia. As espécies pertencem ao gênero *Bokermannohyla* e foram coletadas em áreas pouco exploradas da Serra do Espinhaço durante a realização das expedições de campo para este estudo.

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Capítulo 1

Anuran diversity and conservation deficits for the greatest Brazilian mountain range: a gap analysis based on species distribution models.

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Anuran diversity and conservation deficits for the greatest Brazilian mountain range: a gap analysis based on species distribution models.

Abstract

We investigated patterns of richness and endemism of anurans in the most extent Brazilian mountain range and evaluate species conservation trends by accessing the adequacy of protection (representation) and habitat loss of each endemic species. We used a large point locality data set and three distribution modeling technics to produce detailed maps of the predicted range of 47 Espinhaço range anuran species. Then, we compared predicted distributions with the current Brazilian reserve system to assess the adequacy of protection (based on species-specific representation targets) for each endemic species and detect gaps in protection. After that, we accessed the amount of habitat already lost within species range. Finally, we verified how endemic species life-history traits are related to their range-size, habitat loss, protected range and adequacy of protection. Species richness, endemism richness and endemism levels aggregated into two main hotspots localized in the southern portion of the range and in the Chapada Diamantina at its northern portion, but less inclusive areas of great richness and endemism levels were also pinpointed. We reported one of the most worrying cases of species representation in reserves ever reported, considering gap analyses performed at different continents and various taxonomic groups (87% of the endemics are not properly protected). The vast majority (94%) of species have been already affected by habitat loss, in a way the fulfillment of the protection target of nine narrowly endemic species became unreachable. Forest anurans lost more of their range than species that reproduce in open habitats. Considering multiple criteria (species richness, endemic richness, weighted endemism, habitat loss indexes and representation deficit indexes)

we pinpoint several areas of special concern for habitat protection. Our findings also highlight the urgent need to extend field efforts towards exploration on other Neotropical mountains because of their great relevance for the scientific research and biodiversity conservation.

Introduction

The creation and maintenance of protected areas (PAs) is a world-wide key strategy to protect endangered biodiversity (Bruner et al., 2001; Chape et al., 2005). For this purpose, over the years, countries have established (though at different rates) a reserve network which accounts for nearly 13% of the global territory (Jenkins & Joppa, 2009). However, in the absence of spatially explicit data, it is unlikely that a network of protected areas can be effectively designed so as to ensure proper biodiversity protection (Brooks et al., 2004a; Pressey, 2004). Thus, understanding the spatial patterns of species richness and endemism provide the essential first step of systematic conservation planning (Margules and Pressey, 2000). Nevertheless, our knowledge about how many species inhabit Earth and their geographical distributions remains incipient and plagued by the so-called, respectively, Linnean and Wallacean shortfalls (Lomolino, 2004; May, 2010; Mora et al., 2011). These shortages are mostly problematic in the tropics (Kress et al., 1998; Bini et al., 2006), especially in mountain ranges where many new species and genera of vertebrates are still described at a rapid pace (e.g. Rodrigues et al., 2009; Percequillo et al., 2011) and individuals records are fairly sparse and spatially biased owing to their remoteness and extremely difficult access. The most extent South American mountain range besides Andes, the Espinhaço range at eastern Brazil, is no exception to the rule and is characterized at the same time by an extremely rich and endemic biota and huge knowledge gaps (Giulietti et al., 1997; Echternacht, 2011).

Several studies have demonstrated that PAs often do not represent the biodiversity properly (Scott et al., 1993; Rodrigues et al., 1999; Margules and Pressey, 2000) as reserve locations are frequently chosen opportunistically and without targeting on one of its major goals—namely, protecting species. In a world-wide assessment 74% of terrestrial vertebrates species were found not to meet their representation targets stressing global reserve system is far from complete and have yet to be augmented (Rodrigues et al., 2004). This picture is even more severe for amphibians which are markedly less well covered than other taxa because they have much smaller range sizes (increasing the probability of falling through the network) and because few reserves have been created with specific consideration of amphibians, while mammals and birds are more often taken into account (Rodrigues et al., 2004). Not by chance, amphibians are also the terrestrial vertebrates most at risk of extinction: at least 37% are classed as Vulnerable, Threatened or Endangered (IUCN, 2012). This scenario is certainly optimistic, because the conservation status of about 25% of species remains unknown (IUCN, 2012) and because many taxa are still not known (Bini et al, 2006; Giam et al., 2012).

Gap analysis is a systematic planning tool which aims to assess the extent species, vegetation types or biomes are adequately protected by an existing reserve network, by defining representation biodiversity targets (Scott et al., 1993; Jennings, 2000). Representation targets play a major role in systematic conservation planning by providing clear purposes for implementing conservation actions particularly for decisions regarding area prioritization (Margules and Pressey, 2000; Cowling et al., 2003). Species-specific targets should ideally be defined as the percentage of the original range required to allow species persistence (Rodrigues et al., 2004). Therefore, a solid gap analysis should rely on spatially explicit data which must include species detailed distributions (not to be confused with gross delineations of range limits) and also account for previous habitat losses (Jennings, 2000). However, if the current distribution of an element is already hard to known (especially in the tropics) the historic distribution is even more difficult.

A wide range of methods has been used for estimating species distributions (Graham & Hijmans, 2006). Within this broad spectrum of techniques the use of species distribution models (SDM) is an alternative to overcome the lack of current and historical knowledge about species distributions (Elith and Leathwick, 2009). These models have recently increased in sophistication and prediction accuracy and can even perform satisfactorily for species known from few localities (Elith et al., 2006, Hernandez et al., 2006). Niche-based models estimate the relation between a species and its environment and then predict a distribution based on the occurrence of the identified suite of environmental variables across the landscape under study (Elith and Leathwick, 2009). Although their caveats (Wiens et al., 2009; Warren, 2012), SDM have been successfully applied to a variety of questions in ecology, evolution, and conservation (Araújo and Peterson, 2012).

The Espinhaço range (known as *Serra do Espinhaço*) represents the most extensive and continued orogenic belt of the Brazilian territory (Almeida-Abreu & Renger, 2002). Unlike other main mountain ranges of central and eastern Brazil that are fully embedded in a single biome (Atlantic forest or Cerrado) the Espinhaço range is located in the transition zone between these two Neotropical hotspots and it is still the only large mountain range embedded within the Caatinga semi-arid biome (Fig. 1). From a continental perspective, the Espinhaço can be considered an island, because it is isolated from other large blocks of South American highlands (Andes, Pantepui, and southern Brazilian ranges). Due to this isolation, the Espinhaço harbours a unique biota with many endemic genera and species of plants (Giulietti & Pirani, 1988). The Atlantic forest and the Cerrado are among the most diverse and threatened regions of the world (Mittermeier et al., 2005). Recent estimates based on satellite remote sensing shows that between 84% and 88.6% of the Atlantic forest and approximately 55% of the Cerrado's original vegetation has been removed (Machado et al., 2004; Ribeiro et al., 2009). The Caatinga conservation status is not better. Between 30.4% and 51.7% of this semi-arid biome has been altered by human activities, which conservatively rank this biome as the third most heavily impacted in Brazil (Leal et al., 2005). Owing to its steep relief, Espinhaço higher lands remained less altered than adjoining lower lands offering a unique possibility to still conserve part of the original biodiversity of these three threatened Neotropical biomes. Nevertheless, the extreme high number of threatened narrowly endemic species in these habitats (MMA, 2008; IUCN, 2012) and the increasing pace of human driven disturbance activities (Jacobi et al., 2007; Versieux & Wendt, 2007; Barbosa et al., 2010) claim for urgent conservation actions.

In this paper we depict for the first time the spatial patterns of anuran richness, endemism and collection effort across the entire Espinhaço range based on a large data set. We benefit from SDM to generate range maps of 47 endemic species. Then, we compare predicted distributions with the current Brazilian reserve system to assess the adequacy of protection (representation) for each endemic species and detect eventual gaps in protection. After that, we superimpose these maps to a map of Brazilian vegetation remnants to access the amount of habitat already lost within species range. Finally, we verify how endemic species life-history traits are related to their range-size, habitat loss, protected range and representation target achieved. Our ultimate goal is to provide multiple relevant criteria that will be useful to assist upcoming species conservation status reassessments and pinpoint areas of high conservation priority.

Methods

Data collection

We gathered a database on anuran distribution in the Espinhaço range based on museum specimen inspection and field surveys. We limited our revision to localities placed within an elevation threshold of 500 m a. s. l. around the range. All museum specimens' identities were checked by physical examination. We examined 17,240 specimens deposited in seven Brazilian collections (see acknowledgments). To fill some sampling gaps we carried out from 2007 to 2011 field surveys in 14 localities accounting for 140 days of fieldwork and 4,466 georeferenced sampled anurans. When available, we used geographical coordinates from museum databases, and in other instances, precise locations were obtained directly from collectors. When record coordinates were not available in museum databases, we approximated point localities from locality descriptions using Google Earth® and the Geoloc tool (available in http://splink.cria.org.br). When these information where not available, locations were represented by municipality administration center. We classified species according to their breeding habitats based on field data and literature accounts.

Measures of species richness, endemism and collection effort

We mapped, based on point localities data, the geographic distributions of all Espinhaço anuran species. The distribution of all species was then overlaid into a single map with a spatial resolution of 0.3° grid cell using the software ArcGis™ 10.0, depicting patterns of anuran species richness and endemism richness across the mountain range. Collection effort was inferred by summing the number of collected specimens per grid cell.

To measure endemism we calculated the weighted endemism index (WE) following Williams & Humphries (1994), Slatyer et al. (2007) and others. WE counts all species in a given area, but weighting each by the inverse of its range, assigning high weights to small ranged species, and progressively smaller weights to more widespread species. Thus, a species with 1000 km^2 of range-size would have a WE 10 times bigger than a species with a range of 100,000 km^2. Species range-size was predicted by modeling species distributions (see topic below).

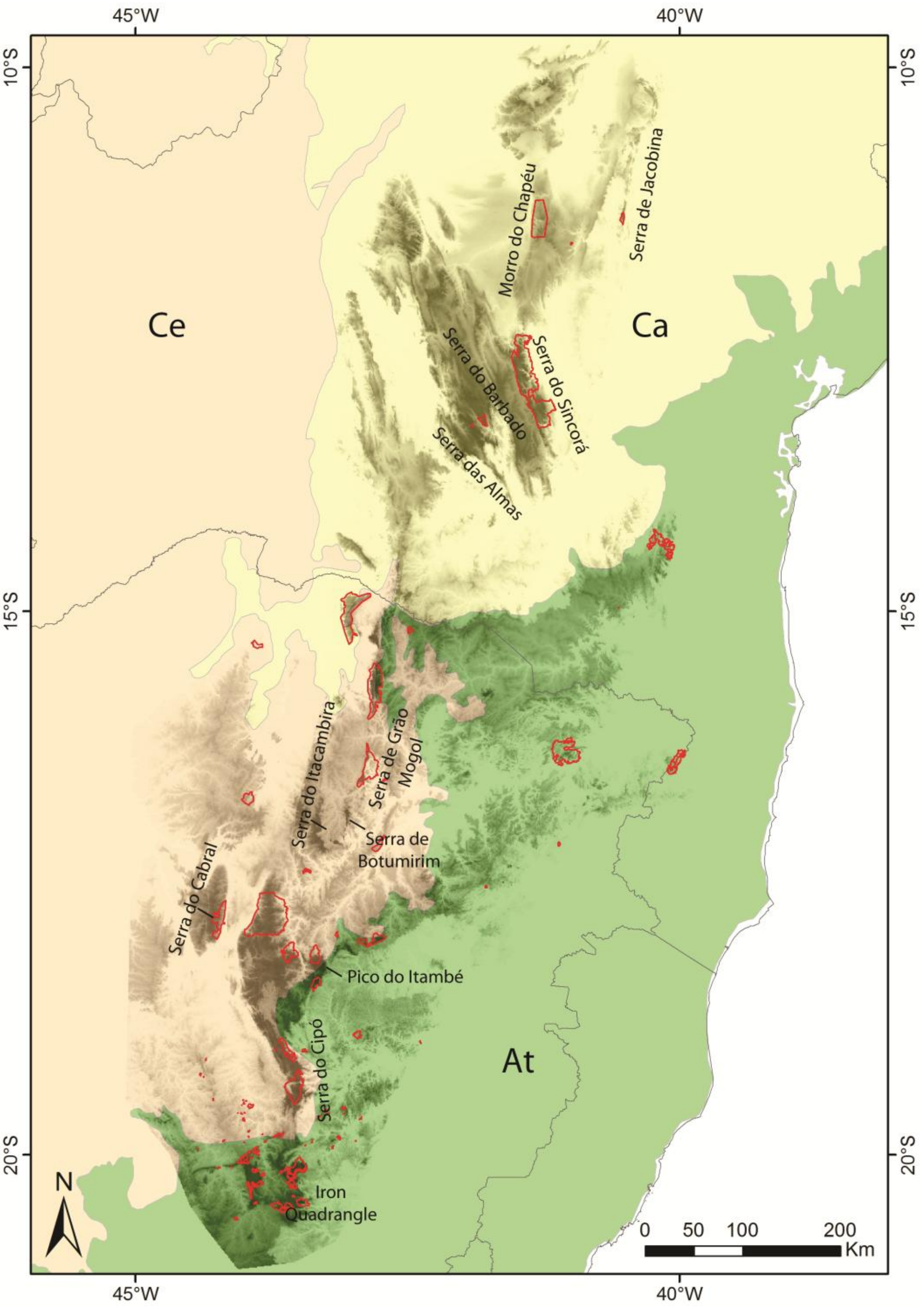

Fig. 1 General location of the Espinhaço range in eastern Brazil, depicting main landscape features mentioned in the text and adjoining biomes: Atlantic forest (At), Cerrado (Ce), and Caatinga (Ca). Protected areas are outilined by red. Darker gray tones represent increasing elevations from 785 to 2072 m a. s. l. Gray lines indicate state limits.

Environmental data and distribution modeling

Environmental variables used to produce niche-based distribution models included climatic, topographic and sensing-derived vegetation variables at a 30″ (1 km^2) spatial resolution. The integration of climatic-topographic variables with remote sensing-based variables is likely to produce more accurate spatial predictions of species distribution (Zimmermann et al., 2007; Buermann et al., 2008). We used enhanced vegetation index (EVI) derived from MODIS reflectance as a proxy of vegetation structure which in turn may encompass a suite of small-scale habitat characteristics (e.g. microhabitat and microclimate) known to strongly affect the suitability of habitat for anurans (Blaustein et al., 1994). To account for EVI annual variation we calculate the mean EVI values of the wettest (January) and driest month (July) from 2000 to 2010. We included in our SDMs only variables weakly correlated ($r < 0.8$) for the study area. This procedure was done to avoid or minimize overparameterization of the models with redundant variables. Therefore, from a set consisting of 19 bioclimatic variables relating to temperature and precipitation, two topographic (i.e. slope and altitude), plus EVI values, we included in the models seven variables namely, temperature seasonality, temperature annual range, annual precipitation, precipitation seasonality, slope, mean January EVI (2000 – 2010), and mean July EVI (2000 – 2010). Climatic variables were downloaded from the Worldclim data base (Hijmans et al., 2005; http://www.worldclim.org/); topographical variables were from the shuttle radar topography mission (http://srtm.csi.cgiar.org/), and EVI values from the US Geological Survey's (http://glovis.usgs.gov/).

Three modelling methods with distinct logics and increasing levels of complexity were used to generate predicted distribution maps of each 47 endemic species: the

Euclidean distance algorithm (ED), with distances being measured to the closest point; the Mahalanobis distance algorithm (MD), with distances being measured to the average of all presence points; and the machine-learning maximum entropy model Maxent (Phillips et al., 2006). The distance-based models were chosen due to their conceptual simplicity and because they do not need information about absences to determine the suitable conditions for a given species. They measure environmental–climatic similarity of characteristics of each species' occurrence as Euclidean or Mahalanobis distances to the nearest or mean of the available climatic space (Farber & Kadmon, 2003). Also, the ED was selected owing to the presence of species with very small sample within our data set which could not to be modelled with other algorithms (e.g. Siqueira et al, 2009). Maxent was chosen because it also has been shown to work better than other approaches with small samples (Hernandez et al., 2006; Pearson et al., 2007; Wisz et al., 2008). We did not carry out MD and Maxent projections for species with less than 18 and five occurrence points, respectively. ED projections had no sample size restrains. Distance-based methods were implemented by the package openModeller Desktop 1.1.0 (http://openmodeller.sourceforge.net/). Maxent 3.2.4 was used to run the maximum entropy models (Phillips & Dudik, 2008).

To estimate the range-size of species, we converted MD and Maxent models continuous outputs into presence/absence maps by applying the lowest presence threshold (LPT). Because ED distances were measured to the closest point rather than to the average of all points, allowing us to deal with very small sample sizes, we could not have applied the traditional LPT threshold. Thus, in order avoid the use of arbitrary thresholds upon the ED outputs we generated, for species with five or more occurrence points, new models each of them with an exclusive subset of points, being one of the points removed from the input data set each round, in a Jackknife resampling method.

This procedure was repeated such as the number of replicates models equals the number of available occurrence points. Then, for each model we extract the suitability values of the pixel corresponding to the removed point. Finally, the minimum value obtained within all models was assumed as the LTP thresholds and was applied to the full model. For species with less than five points (modeled only with ED) we applied an arbitrary threshold, as there was no other available alternative, where only pixels with suitability of occurrence above 0.7 were considered as potentially suitable for the species and therefore were included in the prediction. Applying a high threshold will reduce the risk of selecting sites with low suitability for individual species what is especially desired for gap analysis and other conservations purposes.

Because models may yield different outputs (Loiselle et al., 2003; Thuiller, 2004; Araújo et al., 2005), it is better to integrate results across multiple methods (Araújo & New, 2007). We used an ensemble-forecasting approach (Araújo and New, 2007) in order to deal with models variability and uncertainty and to obtain the central tendency of predicted distributions. For species which the number of occurrence points allowed the use of two (≥ 5 points) or three (≥ 18 points) modeling algorithms we made an ensemble forecast to reach a consensus scenario among the two or three models, respectively. We carefully analyzed each species consensus distribution and excluded from the predicted range polygons corresponding to disjoint areas where a given species is well known not to occur (Swenson et al., 2012). This was especially useful, for example, to exclude occurrences of southern Espinhaço endemics predicted into its northern portion where they are known not to occur, being sometimes replaced by a closely related taxon.

Criteria for gap and habitat loss analysis

We carried out gap analyses considering the projected distribution of the 47 endemic anuran species. We performed two analyses: one with all categories of reserves including both strictly protected (e.g. national parks, state parks, equivalent to IUCN category II) and sustainable use reserves (equivalent to IUCN category V), herein ‘all reserves’, and another only with strictly protected reserves. We did not include the Brazilian reserve category ‘Area of Environmental Protection’ within the all reserves analyses because conversion of natural land cover for low-intensity type activities (e.g. extensive cattle breeding) or localized intense type (e.g., mining and urban settlements) in these areas are generally allowed. We judged this reserve category, the way they work in the studied area, if not in entire Brazil, bring so few protection to an area that it could not be considered as a species protection surrogate. This category can also occupy broad extensions within the studied area (especially at its southern portion) and so would bias the amount of representation targets achieved by species. We overlapped predicted distributions with the current map of Brazilian protected-area system to access the adequacy of protection (representation) for each species and detect eventual gaps in protection. Shape files of Brazilian protected areas were downloaded from IBGE webpage (Brazilian Institute of Geography and Statistics; http://mapas.ibge.gov.br/) and consist of federal, state and municipal reserves, implemented until 2011.

Representation is the percentage of area of a species range included within protected areas, in order for the species to be considered covered (Rodrigues et al., 2004). Representation target is a parameter commonly used in conservation planning to assess adequacy of protection (Margules and Pressey, 2000; Margules and Sarkar, 2007). We established a species-specific representation target depending on the area occupied by each species. For very narrowly distributed species (area of occupancy < 500 km^2), the representation target is 100% of the range; for widespread species (< 25,000 km^2), the target is 10%. For species with area of potential presence of intermediate size (> 500 < 25,000 km^2) the target was interpolated between these two extremes using a linear regression on the log-transformed area occupied, following the procedure proposed by Rodrigues et al. (2004). A species was considered a “gap species” if less than 20% of its representation target was met, “partially protected” if its representation target is only partially met (more than 20% less than 90%), and “protected” if more than 90% of its representation target was achieved. We create an index which, in a way similar to the WE, counts all species (no matter how represented) in each cell but weighting each by the inverse of the percentage of the representation target it had achieved. We term this measure Representation Deficit Index (RDI). Thus, species with higher representation deficit index are worse protected and more likely to be exposed to habitat loss.

We superimpose each species’ predicted distribution to the latest version of the maps of Brazilian vegetation remnants (i.e. Atlantic forest, Cerrado and Caatinga) available at the Brazilian Biomes Deforestation Monitoring Project webpage (http://siscom.ibama.gov.br/monitorabiomas/index/) to access the amount of their range already affected by habitat loss. In order to ensure species more affected by habitat loss to have an increased relative importance in relation the lesser affected species we create a simple index. The Habitat Loss Index (HLI) weights species more affected by conversion of natural landscapes in to unsuitable habitats by squaring the proportion of its predicted range already lost. To obtain a habitat loss score for a cell, these weights are summed for all species occurring in the cell.

Statistical analyses

Generalized linear models (GLMs) were built to evaluate the effect of physiognomy (forested/open), water flow (lotic/lentic), and hydroperiod (temporary/permanent) of breeding habitat (explanatory variables) on the species predicted range and latitudinal range (response variables). We also applied GLMs to verify the effect of the same set of reproductive habitat variables plus the species predicted range on the percentage of range under protection, the percentage of the representation target achieved and the percentage of original range already affected by habitat loss. The minimal model was constructed by removing non-significant explanatory variables ($p > 0.05$) from the complete model in all the analyses described above. All models were developed using R software 2.10 (R Development Core Team, 2010), followed by residual analyses and assessment of error distribution adequacy (Crawley, 2007).

Results

Species richness, endemism and collection effort

The Espinhaço range has high anuran species richness, including endemic, widespread, and species typical from each of the three biomes it is embedded in (i.e. Atlantic Forest, Cerrado and Caatinga). We recorded 162 anuran species, belonging to 15 families, and 37 genera (Appendix I, supplementary material). Families with the highest number of representatives were Hylidae (78), Leiuperidae (22), Leptodactylidae (16), Cycloramphidae (12) and Brachycephalidae (10). The monotypic genus *Rupirana* and other 46 (ca. 29%) taxa are endemic. The stream dweller *Bokermannohyla pseudopseudis* species group, which is endemic to central and eastern Brazilian mountains showed a particularly high level of endemism in the Espinhaço. Six out of ten known species of this group are Espinhaço endemics. Thirteen (ca. 28%) out of the 47 endemic species are undescribed but easily diagnosable new taxa. Some other verified specimens could not be assigned to any described species, but due to taxonomic problems concerning many Neotropical anuran taxa, we assume a more conservative criterion and did not considered them as multiple undescribed species.

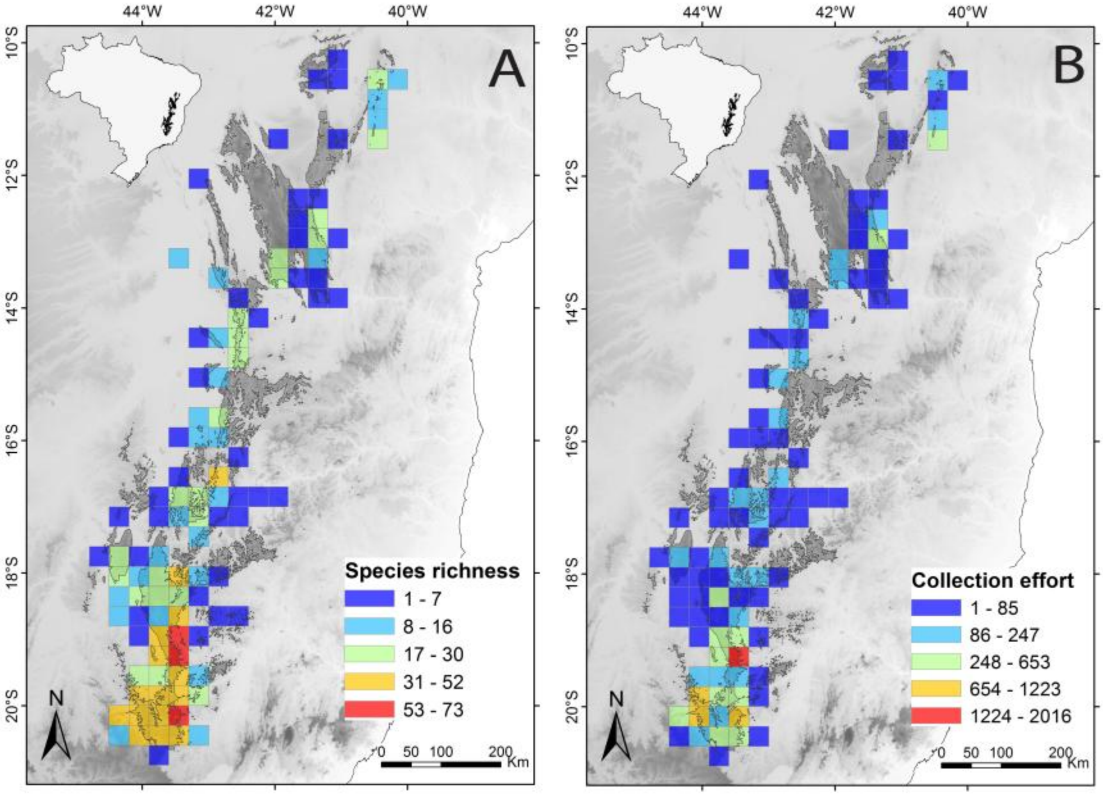

Fig. 2 (A) Number of anuran species per unit area (0.3° x 0.3° cell) (B) collection effort by means of the number of museum specimens records in the Espinhaço range in the states of Minas Gerais and Bahia, Brazil.

The maximum values for anuran species richness were found in southern portion of the Espinhaço range, in areas corresponding to the Serra do Cipó and the eastern Quadrilátero Ferrífero, in the state of Minas Gerais where a single grid cell could have up to 73 species (Fig. 2A). In addition, isolated cells of moderately high richness exist in the northern edge of the Diamantina Plateau, and in the Serra de Grão Mogol, in the north of Minas Gerais. Species richness decreases towards northern region, in areas corresponding to the small mountain chains of northern Minas Gerais and Chapada Diamantina, in the state of Bahia.

Mapping the number of museum specimens collections per grid cell depicts a sampling bias towards the southern portion of the mountain range, where the Espinhaço most representatives anuran collections (UFMG and MCNAM) are located and historical collection were made by 1960-70 (Fig. 2B). Species richness and collection effort maps exhibit relatively congruent distribution patterns (Fig.2A, B). However, grid cells with the greatest richness in Espinhaço do not overlap completely with the collection effort pattern.

The raw data and modeled endemism richness followed the same overall richness pattern with maximum values located in areas corresponding to the range's southernmost portion (Fig. 3A, B). Relative low values for anuran endemic richness were also found in areas corresponding to the small mountain chains of northern Minas Gerais. Conversely, endemic richness increases to moderate levels in the southern portion of Chapada Diamantina region, in the state of Bahia but again, decreases northwards in areas with lower altitudes.

Weighted endemism highlighted two narrowly distributed hotspots in the eastern slopes of Serra do Cipó and in the Pico do Itambé (Itambé summit). Three other areas with moderate to high endemism levels were predicted to occur in the Serra do Cabral, in the western most portion of the Espinhaço in the state of Minas Gerais, Serra das

Almas-Barbado complex and Serra do Sincorá, both at the southern portion of Chapada Diamantina.

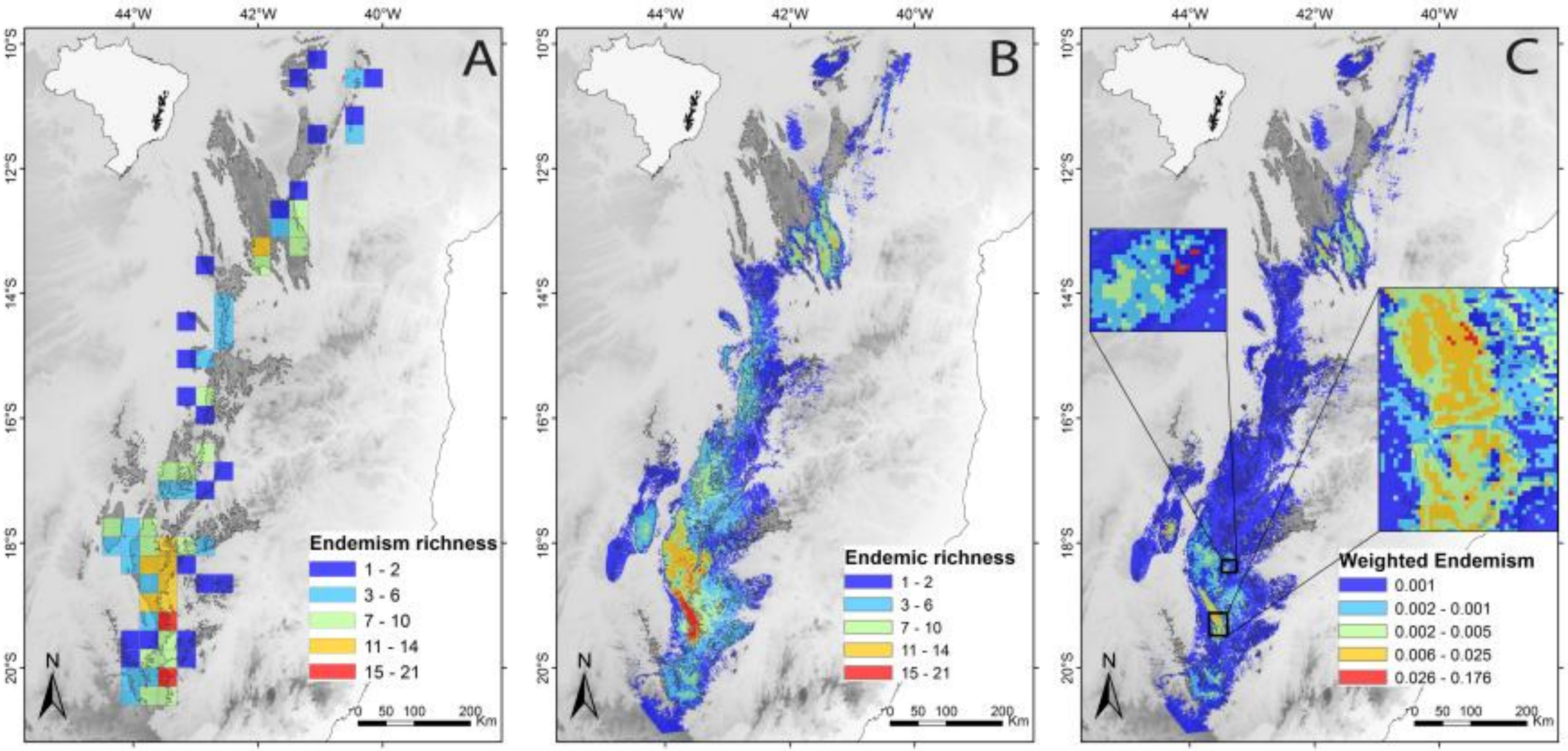

Fig. 3 (A) Number of anuran endemic species per unit area (0.3° x 0.3° cell) based on the raw data (B) number of endemic species based on the species distributions models (C) weighted endemism index in the Espinhaço range in the states of Minas Gerais and Bahia, Brazil. Zooms highlight the Pico do Itambé summit (left) and the Serra do Cipó (right) the regions with the greatest values of weighted endemism index.

Gap and range loss analysis

The current Brazilian reserve network within the Espinhaço range failed to ensure the representation of most of its endemic anuran species (Fig. 4). For all reserves our models identified the majority of taxa analyzed are gap (17, 36%) or partial gap species (24, 51%) (Fig. 4). Only six species are properly protected. Furthermore, in the strictly protected reserves seven (15%) species achieved less than 5% of its representation targets including two southwestern Chapada Diamantina endemics which neither have observational occurrences within reserves nor were predicted to occur in such areas (*Bokermannohyla flavopicta* and *Pseudopaludicola* aff. *mineira*) and two southeastern endemics which also have no records within protected areas (*Aplastodiscus* aff. *cavicola* and *Sphaenorhynchus* aff. *surdus*). Considering both reserves systems more than half of partial gap species reached less than 50% of their protection targets (Tab. 1). The area with the highest values for the representation target index was located in the Espinhaço southern portion at the eastern slopes of the Diamantina Plateau, corresponding to its forested slopes (Fig.5B).

The predicted range was found to affect positively the percentage of the representation target achieved in both the strictly protected ($p=0.002$) and all reserves ($p=0.002$). However, conflicting examples could be found among narrowly endemic species (range < 2500 km^2) for which the percentage of the target achieved varied from nearly zero (e.g. *Aplastodiscus* aff. *cavicola* and *Sphaenorhynchus* aff. *surdus*) to almost 100 (e.g. *Crossodactylodes* sp., a high altitude species with very limited distribution which is entirely inside a State Park) (Fig. 4). We found the percentage of the representation target achieved in both the strictly and all reserves was not affected by reproductive habitat variables ($p>0.05$).

The vast majority (94%) of species had already been affected by habitat loss (Tab. 1). Forty five percent (44) of the anuran endemics lost between 20 and 40% of their original range, whereas 17% (8) lost more than 40%. Land use alone has already decreased the range of 29 species (62%) by at least 20%, of which eight has already lost more than 40% (Table 1). Forest anurans lost more of their range (x=34.9%, SD=15.6, min=11.7%; max=56.7%; n=13; p=0.003) than species that reproduce in open (x=19.4%, SD=12.5, min=0%; max=59.1%; n=27) or in both habitats physiognomy (x=26.7%, SD=6.4, min=18.3%; max=36.1%; n=5), which in turn did not differ from each other (p>0.05). Seven out of the eight species most affected by habitat loss are forested species. *Aplastodiscus* aff. *cavicola* and *Sphaenorhynchus* aff. *surdus* were the most affected species. Accordingly, the maximum values for the habitat loss index were found in the meridional portion of the Espinhaço range, in areas corresponding to its Atlantic forested slopes (Fig. 5A). Habitat loss was not affected by breeding habitat water flow and hydroperiod (p>0.05), suggesting that despite higher in closed canopy habitats it has not occurred alongside streams, ponds or puddles more than expected by chance.

We did not find a significant relationship between life-history traits (i.e. physiognomy, water flow, and hydroperiod of the breeding habitat) and the range-size or latitudinal range of the endemic species (P >0.05). Neither the breeding habitat features nor the range were found to affect the percentage of the range protected considering both reserves systems (P >0.05).

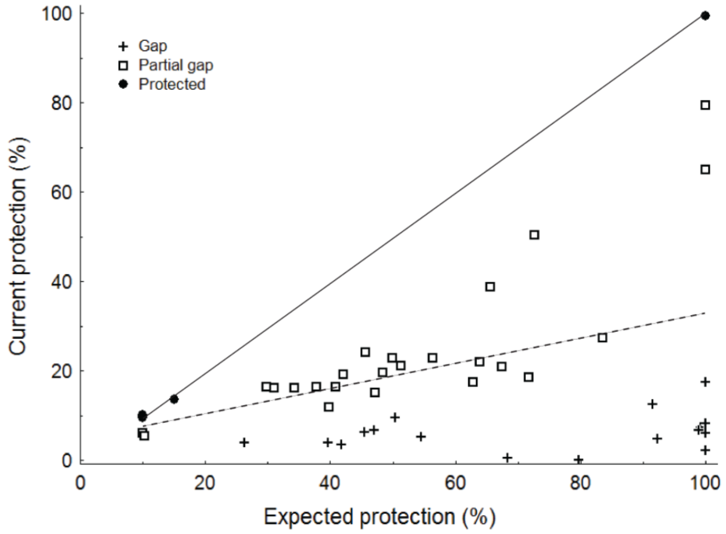

Fig. 4 Relationship between percentage of current (dashed line) and expected protection (target) (continuous line) for 47 Espinhaço range endemic anuran species, depicting gap, partial gap and protected species, considering all reserves system.

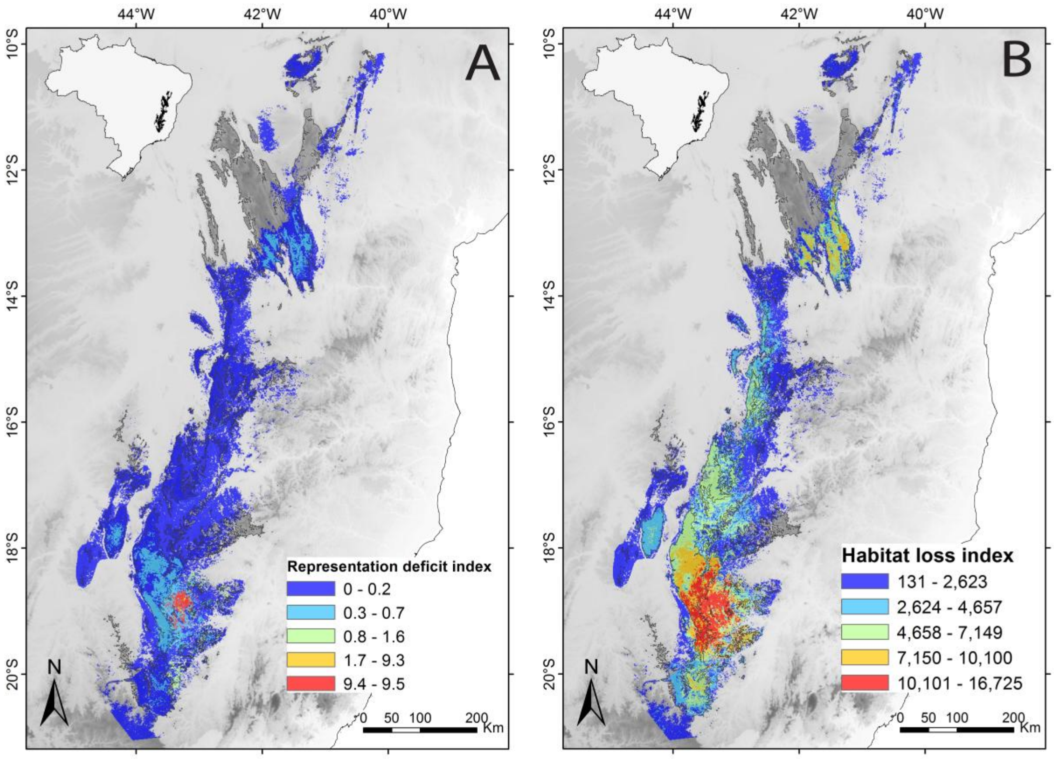

Fig. 5 (A) Representation deficit index (B) habitat loss index for endemic anuran species in the Espinhaço range in the states of Minas Gerais and Bahia, Brazil.

Table 1. Spatially independent points (1 km x 1 km), estimated range (km^2), percentage of range converted for anthropogenic use, number of observational occurrences within all reserves categories, representation targets, percentage of range overlapping Brazilian reserves (strictly protection reserves and all reserves), percentage of the representation target achieved (strictly protection reserves and all reserves), protection status, and conservation status of 47 Espinhaço range endemic anurans.

Taxon	Points	Range (km^2)	Habitat loss (%)	Occurrence within reserves	Target (%)	Protection in strictly protected reserves (%)	Protection in all reserves (%)	Target achieved (%) - stricly protected	Target achieved (%) - all reserves	Protection status - all reserves	IUCN (2011)	Brazil (2003)
Crossodactylodes sp.	1	6	0.0	1	100	99.3	99.3	99.3	99.3	protected	-	-
Physalaemus aff. *rupestris*	1	46	12.3	0	100	15.7	17.5	15.7	17.5	gap	-	-
Physalaemus deimaticus	1	168	0.4	1	100	65.0	65.0	65.0	65.0	partial gap	DD	DD
Scinax pinima	1	240	0.0	0	100	8.2	8.3	16.2	8.3	gap	DD	DD
Bokermannohyla juiju	3	322	8.3	1	100	79.4	79.4	79.4	79.4	partial gap	-	-
Scinax cabralensis	3	329	22.4	1	100	2.2	2.2	2.2	2.2	gap	DD	-
Fritiziana aff. *fissilis*	2	337	1.8	2	100	4.0	6.2	4.0	6.2	gap	-	-
Bokermannohyla sagarana	5	516	18.3	1	99	7.4	7.4	7.5	7.5	gap	-	-
Pseudopaludicola aff. *mineira*	6	526	16.6	0	99	0.0	6.7	0.0	6.8	gap	-	-
Bokermannohyla flavopicta	6	698	23.1	0	92	0.0	4.8	0.0	5.2	gap	-	-

Physalaemus erythros	4	722	7.9	2	92	9.2	12.6	10.1	13.8	gap	DD	-
Hypsiboas cipoensis	12	1023	1.0	3	84	27.3	27.4	32.6	32.8	partial gap	NT	LC
Aplastodiscus aff. *cavicola*	4	1208	56.7	0	80	0.1	0.1	0.1	0.1	gap	-	-
Bokermannohyla itapoty	10	1641	18.0	1	73	50.5	50.5	69.5	69.5	partial gap	LC	-
Bokermannohyla martinsi	15	1706	26.6	6	72	9.1	18.6	12.7	25.9	partial gap	LC	LC
Sphaenorhynchus aff. *surdus*	2	1977	59.1	0	68	0.2	0.5	0.2	0.8	gap	-	-
Pristimantis aff. *ramagii*	5	2060	24.6	2	67	19.4	21.0	28.8	31.2	partial gap	-	-
Rupirana cardosoi	9	2225	23.4	1	66	38.7	38.7	58.9	58.9	partial gap	NT	LC
Physalaemus evangelistai	9	2404	8.7	6	64	18.1	22.0	28.3	34.5	partial gap	DD	DD
Phasmahyla jandaia	7	2511	21.2	5	63	14.0	17.4	22.3	27.7	partial gap	LC	LC
Scinax sp. (clade *ruber*)	18	3340	23.6	2	56	21.9	22.9	8.2	40.6	partial gap	-	-
Hylodes uai	7	3605	41.7	4	55	1.6	5.2	3.0	9.4	gap	DD	LC
Scinax aff. *curicica*	7	4147	27.6	1	51	20.3	21.2	39.5	41.4	partial gap	-	-
Scinax machadoi	8	4326	27.3	4	50	8.2	9.5	16.2	18.8	gap	LC	LC
Pristimantis sp.	11	4398	24.4	0	50	21.9	22.9	43.8	45.8	partial gap	-	-
Bokermannohyla nanuzae	23	4724	11.7	6	48	19.7	19.7	40.7	40.7	partial gap	LC	LC
Proceratophrys minuta	6	4958	36.1	2	47	15.1	15.1	32.0	32.0	partial gap	-	-
Bokermannohyla diamantina	9	4996	25.3	1	47	6.0	6.8	12.8	14.4	gap	DD	-
Leptodactylus gr. *fuscus*	9	5299	27.7	1	46	23.2	24.1	50.7	52.7	partial gap	-	-
Bokermannohyla aff. *feioi*	11	5344	51.5	2	45	3.0	6.4	6.5	14.1	gap	-	-
Strabomantis aramunha	13	6197	28.7	2	42	18.6	19.2	44.2	45.7	partial gap	DD	-
Pleurodema alium	1	6260	21.1	0	42	3.6	3.6	8.6	8.7	gap	-	-

Bokermannohyla oxente	32	6533	27.5	2	41	16.0	16.4	39.1	40.2	partial gap	LC	-
Hypsiboas botumirim	19	6853	19.4	5	40	11.7	11.8	29.3	29.7	partial gap	-	-
Physalaemus orophilus	10	6880	50.8	2	40	2.6	3.9	6.7	9.8	gap	-	-
Phyllomedusa megacephala	12	7474	10.4	3	38	16.4	16.4	43.3	43.5	partial gap	DD	LC
Proceratophrys cururu	7	8721	13.9	5	34	16.3	16.3	47.5	47.6	partial gap	DD	LC
Pseudopaludicola mineira	24	10054	12.4	6	31	16.1	16.2	52.1	52.2	partial gap	DD	LC
Leptodactylus camaquara	26	10590	17.0	8	30	16.1	16.5	54.2	55.4	partial gap	DD	LC
Hylodes otavioi	4	12324	47.3	1	26	3.9	4.0	14.8	15.1	gap	DD	DD
Crossodactylus trachystomus	19	20097	22.0	8	15	12.7	13.7	84.6	91.3	protected	DD	LC
Scinax tripui	7	24615	45.3	1	10	4.5	5.5	43.1	53.2	partial gap	-	-
Scinax curicica	38	27233	33.2	11	10	9.1	9.9	90.9	99.3	protected	DD	-
Bokermannohyla saxicola	38	28871	27.0	9	10	9.6	9.6	95.8	96.4	protected	LC	LC
Bokermannohyla alvarengai	55	29782	27.2	11	10	9.7	10.3	96.8	102.9	protected	LC	LC
Thoropa megatympanum	72	31846	26.7	11	10	9.6	10.1	96.5	100.5	protected	LC	LC
Scinax gr. *catharinae*	63	85313	40.7	7	10	6.0	6.1	59.9	60.8	partial gap	-	-

Discussion

Species richness and endemism

Our results give the first clear description of current anuran species richness and endemism patterns of an entire Brazilian mountain range. Species richness and endemism levels gathered for Espinhaço range anurans overcomes those previously detected by Leite et al. (2008) review which was based manly in literature records. We added 58 species not listed by Leite et al. (2008) revealing a much more diverse anuran fauna than previously known. The gathering of all these distributional and taxonomy data has allowed the description of several new species (e.g. Canedo et al., 2010; Leite et al., 2011; Leite et al., 2012; Carvalho et al., in prep.; Barata et al., in prep.). Eight endemics were described in the last five years (Cassimiro et al., 2008; Caramaschi et al., 2009; Lourenço et al., 2009; Cassini et al., 2010, Maciel & Nunes, 2010; Leite et al., 2011; Napoli et al., 2011; Leite et al., 2012) nevertheless, as noted by Leite et al. (2012), many Espinhaço endemic taxa still wait for formal description. These results attest the extent of our ignorance concerning Neotropical mountains biota and emphasize the decisive importance of bringing together fine point-locality species data, based on careful revision zoological collections and field surveys designed to cover sampling gaps, prior to conservation planning analyses (Brooks et al., 2004b; Nogueira et al., 2011). It also justifies the funding of extensive research programs with the basic purpose of inventorying and describing new species, especially in poorly known tropical developing regions of the world characterized by high rates of habitat loss and, often, by very high biodiversity.

The only Brazilian biome for which there is an anuran species list recovered by means of similar methodology and therefore subject of comparison is the adjoining

Cerrado. However, the southern portion of the Espinhaço is often included in the Cerrado and therefore part of its fauna is considered not only to happen in this biome but also to be endemic to it (Colli, 2005; Valdujo et al., 2012). The number of species and endemic species recorded herein is equivalent to 80% and 57% of the 204 species and 83 endemic species (excluding the 19 Espinhaço species Valdujo et al. (2012) considered also Cerrado endemics) found in the Cerrado, respectively. Nevertheless, if considered the sixfold Cerrado larger area (2,058,200 km^2) in relation to the range's area (328,186 km^2 above 500 m of elevation) and the expected effect of the species-area relationship the Espinhaço alone seems to have a relative greater anuran species richness and endemism richness than its neighboring savanna-like biome. In fact, a considerable portion of the Cerrado anuran richness, especially endemic species, are found on its southeastern portion in the transition with the Atlantic Forest in regions with greater altitudinal variation which corresponds to the Espinhaço range (Diniz-Filho et al., 2007; Diniz-Filho et al., 2008; Silvano et al., 2011). This pattern was also corroborated for Cerrado squamates reptiles for which altitude was important in predicting species richness (Costa et al., 2007) and endemism richness prevailed in open elevated plateaus, which is the case of Espinhaço, instead in the peripheral depressions (Nogueira et al., 2011). These results suggest not only altitude but also the geographic location of the range between two Neotropical hotspots might be related to the great anuran diversity found at the Espinhaço range.

The number of Espinhaço anuran endemic species documented in the present study largely surpasses those known for any other vertebrate group, including fishes (27, Alves et al., 2008), birds (5, Vasconcelos et al., 2008; Freitas et al., 2012), and mammals (2, Lessa et al., 2008). There is no synthesis about Espinhaço endemic squamates, nevertheless the number of species should be around 12 (FSFL, personal observation). This pattern is similar to that described for tropical Andes (Lynch, 1987; Lynch et al., 1997). In contrast with other vertebrate ectotherms, the better ability to adjust their physiology at lower temperatures at high elevations (Navas, 1996), higher ecophysiological constraints and the low dispersal ability of anurans, the latter supposed to cause geographic isolation and further speciation (Hillman et al., 2009) are likely to be the main factors behind these patterns. Endemic vertebrates were showed to be the most effective surrogates for identifying conservation priorities at an infracontinental scale (Loyola et al., 2007). In this sense, the higher number of endemic anurans in highland systems and its usual narrower distributions when compared to other vertebrates make them possibly one of the best indicator groups for conservation planning analyses within tropical mountain ranges.

It is clear from this study that richness, endemism richness and endemism levels (WE) are not distributed randomly over the landscape, but do aggregate into hotspots localized in the southern portion of the range (Quadrilátero Ferrífero, Serra do Cipó, and Diamantina Plateau) and in the Chapada Diamantina at its northern portion. Why this phenomenon occurs is properly the subject of macroecology and biogeography, and beyond the scope of this paper. However, these hotspots correspond to the largest, highest and most continuous highland islands of the entire range. Accordingly, besides climatic factors commonly used to explain richness patterns across broad scales environmental gradients (e.g. Costa et al, 2007; Diniz-Filho 2008) there may be other variables such as area and degree of isolation playing important roles in determining species richness and endemism in this high altitude topographic islands system.

The decrease in endemism levels between the southern and northern hotspots and northwards Chapada Diamantina is due not only to the lower endemic species richness found there. Most species recorded in these regions despite being endemic are well distributed across the range and therefore contributes little to local WE. This general pattern of species richness and endemism is well corroborated by many Espinhaço plant taxa (Harley, 1995; Pirani et al., 2003; Echternacht et al., 2011a). The positive correlation between overall and endemic species richness and the collection effort suggests this pattern could be biased. However, by modeling endemic species distributions based on extensive specimen-based revision we believe to have reduced this bias (Elith and Leathwick, 2009).

Gap and range loss analysis

The Brazilian reserve network within the Espinhaço range revealed to be very inefficient in conserving its endemic anurans. We reported one of the most worrying cases of species representation in reserves ever reported, considering gap analyses performed at different continents and various taxonomic groups, including anurans (Fjeldså et al., 2004; Maiorano et al., 2006; Catullo et al., 2008, Urbina-Cardona & Loyola, 2008; Ochoa-Ochoa et al., 2009). The extent species are being protected based on species-specific representation targets were accessed only two times in Brazil, both for the Cerrado region. Silvano et al. (2011) found 58% of this savanna-like biome endemic anurans did not achieve 20% of their targets and therefore were considered gap species. However, the range-size thresholds they use for defining targets were far higher than those we use. We applied the same targets they apply and found almost 100% of Espinhaço endemic anurans would have to be considered gap species. A gap analysis concerning this Neotropical hotspot birds showed only 3 (8%) out of 38 endemics are gap species (Marini et al., 2009).

As in any gap analysis, our results depend heavily on the representation target stated, which in turn necessarily have a degree of arbitrariness (Scott, 1993; Jennings, 2000). Rodrigues et al. (2004) while working with most vertebrate groups worldwide set a 100% representation target for species with small ranges (< 1000 km^2), and a 10% target for widespread species (> 250,000 km^2). These thresholds were adopted by several authors for different of animal taxa (e.g. Catullo et al., 2008; Marini et al., 2009). A gap analysis based on a species-specific targets has never been addressed specifically to very small ranged high altitude tropical frogs. We set the representation target to 100% for species with a very narrow distributions (< 500 km^2) to 10% for widespread endemic species (> 25,000 km^2), according to the following rationale. High altitude amphibians have naturally smaller ranges if compared to other vertebrate group (Navas, 1996; see discussion in the topic *Species richness and endemism*). Accordingly, it is expected that a smaller area could support the number of individuals need to assure a frog population persistence over time and space easier than it would be for a well distributed mammal or bird (Jenkins, 1981; Davies et al., 2000). The percentage of the range of a widespread tinny leaf-litter frog that must overlap reserves areas for the species to be protected, for example, is probably not enough for a jaguar. On the other hand, species with small ranges are expected to be more vulnerable to adverse natural events and anthropogenic activities and therefore most prone to extinction (Schemeske et al., 1994; Purvis et al., 2000; Gaston, 2003; Grenyer et al., 2006). Thus, narrow distributed species far from achieving their targets are exactly those most deserving of special conservation efforts.

Whereas species representation perspectives are not encouraging they become even worse in the face of conversion of natural landscape into anthropogenic low suitable habitats. Land use alone has already decreased the original range of nine narrowly endemic species in a way the fulfillment of their protection target became unreachable. Unfortunately, the two species most affected by habitat loss (*Aplastodiscus* aff. *cavicola* and *Sphaenorhynchus* aff. *surdus*), which have already lost almost 60% of their range, are the farthest from reaching their representation targets (less than 1% met), are not known to occur in any reserve, and have their very small observed range within highly threatened regions due to iron ore mining activities (see Jacobi et al., 2007). Additionally, because they were not yet formally described they are not candidates for having their risk of extinction classified by any official initiative (i.e. state, national or global lists) and therefore have no legal protection. These species must be considered critical conservation goals. Habitat loss within their range must not be acceptable and every site they occur is of utmost importance for their conservation.

The predictions we made, even though already worrying, might be considered optimistic due to several reasons. First, we set representation targets lower than usually applied for vertebrates worldwide (e.g. Rodrigues et al., 2004; Catullo et al., 2008; Marini et al., 2009). Second, SDM studies cannot be considered unequivocally true and all models have a degree of uncertainty that must be assumed (Barry & Elith, 2006; Wiens et al., 2009). In an extensive mountain range characterized by topographical and climatic discontinuities leading to various geographical barriers, as it is the case of Espinhaço range (Leite et al., in prep.), SDM outputs concerning organisms with low dispersal capabilities are expected to over predict distributions. Although we excluded from predicted distribution outputs areas a given species is well known not to occur so as to reduce models commission errors, this procedure was limited to localities we know and therefore are of limited reach. This could be the case of the marsupial frog *Fritziana* aff. *fissilis*. This highly specialized tree-frog is known to occur only in the nebular environment of the top of two southern Espinhaço summits where it reproduces exclusively in open-field bromeliad phytotelmata. The SDM predicted it to occur in several other places that despite having similar environmental-climatic conditions, in relation to localities the species is known, do not coincide to summits and therefore are likely to have different micro-climatic conditions, such as nebulosity and wind intensity, or do not have bromeliads that are essential for the frog to occur. Third, management and supervision of many reserves in the tropics, in fact, are not effective in ensuring species persistence making them usually act as ‘‘paper parks’’ (Schwartzman et al., 2000; Sigel et al., 2006; Gaveau et al., 2007). Lastly, montane tropical organism with narrow elevational ranges, such as amphibians, may be thermally specialized and likely to be among the most imperiled species on Earth by global warming (Wake & Vredenburg, 2008; Hagger et al., 2012). For instance, this was especially true for the Espinhaço endemic birds which were predicted to be the most affected species within the Cerrado as a result of projected climate changes (Marini et al., 2009).

Many Brazilian prioritization exercises accounts only for species richness, or few criteria, to locate areas of high conservation priority (e.g. MMA 1999; 2000a, 2000b). However, a desired priority-setting conservation appraisal should rely on multiple criteria, clear targets, and distinct taxonomic groups (Margules & Pressey, 2000). We contributed to Brazilian anurans’ conservation planning by providing five criteria (species richness, endemic richness, WE, habitat loss and representation deficit indexes) that allow us to pinpoint the Espinhaço southeastern Atlantic slopes (notably in the Serra do Cipó, Pico do Itambé and Serra do Caraça), the Serra do Cabral, and the southwestern Chapada Diamantina (Almas-Barbado complex) as areas of special concern for habitat protection as they assemble the highest values for many of the above mentioned layers. Nevertheless, at the core of reserve selection problems is the goal of minimizing the area and cost of the reserve system whilst meeting conservation targets

(Leslie et al., 2003). Accordingly, delineating areas of high conservation priority within a decision theory framework and mathematical algorithms (Possingham et al., 2001) should be considered a future research agenda for the Brazilian highlands so as to provide the best flexible, repeatable, and efficient solutions to spatial allocation problems.

To broaden and add usefulness to the results we found, patterns of distribution, representation and habitat loss should be evaluated for other Espinhaço taxa, especially plants (which accounts for a large amount of endemics). We predict, however, a similar result, because many of them have resembling patterns of distribution with many narrowly endemic species and with overall and endemic richness concentrated at the same regions (Harley, 1995; Rapini et al., 2002; Pirani et al., 2003; Versieux & Wendt, 2007; Echternacht et al., 2011b). Thereby, if the large conservation deficits and high levels of habitat loss found for anurans will also be found for other endemic species, the unique and highly diverse Espinhaço biota might be much more threatened than previously thought. Our findings also highlight the urgent need to extend field efforts towards exploration on other Neotropical mountains because of their great relevance for the scientific research and biodiversity conservation.

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Appendix I

List of the 163 anuran species registered in the Espinhaço range, in the states of Minas Gerais and Bahia, Brazil.

Adelophryne sp., *Adenomera* cf. *thomei, Ameerega flavopicta, Aplastodiscus* aff. *cavicola, Aplastodiscus arildae, Aplastodiscus cavicola, Bokermannohyla* aff. *circumdata, Bokermannohyla* aff. *feioi, Bokermannohyla alvarengai, Bokermannohyla diamantina, Bokermannohyla flavopicta, Bokermannohyla itapoty, Bokermannohyla juiju, Bokermannohyla martinsi, Bokermannohyla nanuzae, Bokermannohyla oxente, Bokermannohyla sagarana, Bokermannohyla saxicola, Ceratophrys aurita, Ceratophrys joazeirensis, Chiasmocleis albopunctata, Chiasmocleis mantiqueira, Chiasmocleis schubarti, Corythomantis greeningi, Crossodactylodes* sp., *Crossodactylus trachystomus, Dendropsophus branneri, Dendropsophus* cf. *giesleri, Dendropsophus* cf. *microps, Dendropsophus decipiens, Dendropsophus elegans, Dendropsophus minutus, Dendropsophus nanus, Dendropsophus oliveirai, Dendropsophus rubicundulus, Dendropsophus seniculus, Dendropsophus soaresi, Dermatonotus muelleri, Elachistocleis cesarii, Eupemphix nattereri, Flectonotus* aff. *fissilis, Haddadus binotatus, Hylodes babax, Hylodes otavioi, Hylodes uai, Hypsiboas albomarginatus, Hypsiboas albopunctatus, Hypsiboas botumirim, Hypsiboas cipoensis, Hypsiboas crepitans, Hypsiboas faber, Hypsiboas lundii, Hypsiboas pardalis, Hypsiboas polytaenius, Hypsiboas semilineatus, Ischnocnema* aff. *juipoca, Ischnocnema* aff. *parva* sp.2, *Pristimantis* aff. *ramagii, Ischnocnema* gr. *lactea, Ischnocnema* gr. *parva, Ischnocnema izecksohni, Ischnocnema juipoca, Pristimantis paulodutrai, Pristimantis* sp., *Ischnocnema surda, Itapotihyla langsdorffii, Leptodactylus caatingae, Leptodactylus camaquara, Leptodactylus cunicularius,* *Leptodactylus furnarius, Leptodactylus fuscus, Leptodactylus jolyi, Leptodactylus labyrinthicus, Leptodactylus latrans, Leptodactylus macrosternum, Leptodactylus mystaceus, Leptodactylus mystacinus, Leptodactylus* gr. *fuscus, Leptodactylus syphax, Leptodactylus troglodytes, Leptodactylus vastus, Odontophrynus aff. americanus, Odontophrynus carvalhoi, Odontophrynus cultripes, Phasmahyla jandaia, Phyllomedusa ayeaye, Phyllomedusa bahiana, Phyllomedusa burmeisteri, Phyllomedusa megacephala, Phyllomedusa nordestina, Phyllomedusa rodhei, Physalaemus albifrons, Physalaemus centralis, Physalaemus* cf. *crombiei, Physalaemus* aff. *rupestris, Physalaemus cicada, Physalaemus cuvieri, Physalaemus deimaticus, Physalaemus erythros, Physalaemus evangelistai, Physalaemus* gr. *signifer, Physalaemus kroyeri, Physalaemus marmoratus, Physalaemus maximus, Physalaemus orophilus, Pleurodema alium, Pleurodema diplolister, Proceratophrys boiei, Proceratophrys cristiceps, Proceratophrys cururu, Proceratophrys minuta, Pseudis bolbodactyla, Pseudis fusca, Pseudopaludicola* aff. *mineira, Pseudopaludicola* cf. *mystacalis, Pseudopaludicola mineira, Pseudopaludicola serrana, Pseudopaludicola* sp.*, Rhinella crucifer, Rhinella granulosa, Rhinella jimi, Rhinella pombali, Rhinella rubescens, Rhinella schneideri, Rupirana cardosoi, Scinax* aff. *curicica, Scinax* aff. *flavoguttatus, Scinax* aff. *perereca, Scinax cabralensis, Scinax camposseabrai, Scinax cardosoi, Scinax carnevallii, Scinax* cf. *x-signatus, Scinax crospedospilus, Scinax curicica, Scinax eurydice, Scinax fuscomarginatus, Scinax fuscovarius, Scinax* gr. *catharinae, Scinax* sp. (clado *ruber*)*, Scinax* sp.2 (clado *ruber*)*, Scinax longilineus, Scinax luizotavioi, Scinax machadoi, Scinax maracaya, Scinax pachycrus, Scinax pinima, Scinax rogerioi, Scinax berthae, Scinax squalirostris, Scinax tripui, Sphaenorhynchus* aff. *surdus, Strabomantis aramunha, Thoropa megatympanum, Thoropa miliaris, Trachycephalus atlas, Trachycephalus mesophaeus, Trachycephalus* *nigromaculatus, Trachycephalus venulosus, Vitreorana* aff. *eurygnatha, Vitreorana* aff. *uranoscopa, Vitreorana uranoscopa.*

Capítulo 2

Anuran distribution patterns in the Brazilian highlands: implications for the delimitation of Espinhaço range areas of endemism and understanding of their evolutionary dynamic.

Leite, F. S. F.; Oliveira, U.; Garcia, P. C. A. (in prep.). Anuran distribution patterns in the Brazilian highlands: implications for the delimitation of Espinhaço range areas of endemism and understanding of their evolutionary dynamic. Manuscrito em preparação que será submetido ao periódico *Journal of Biogeography*.

Anuran distribution patterns in the Brazilian highlands: implications for the delimitation of Espinhaço range areas of endemism and understanding of their evolutionary dynamic.

ABSTRACT

Aim We evaluated patterns of endemism for amphibian anurans along the most extent Brazilian mountain range aiming to: (1) identify areas of endemism (AE) and explore their hierarchical relationships, (2) investigate whether AE are bounded by climatic and topographical barriers, and (3) investigate the potential distribution of AE during the Quaternary climatic fluctuations determining if they were historically stable areas.

Location Espinhaço Range, the greatest Brazilian mountain range extending about 1000 km between two global biodiversity hotspots, the Atlantic forest and the Cerrado.

Methods We compiled species occurrence records via revision of museum collections and extensive fieldwork. Areas of endemism were identified using Geographic Interpolation of Endemism, a recently proposed method that waives the use of grid cells. We used a suite of multivariate statistics tools (i.e. cluster analysis, principal component analysis and discriminant analysis) to explore the hierarchical relationships, ordination and discrimination of AE regarding their species composition and climatic features. To verify if AE are bounded by climatic barriers we used Monmonier's algorithm. We modelled the potential distribution of each AE by implementing a Mahalanobis distance algorithm across three time projections: current, mid-Holocene (6 kyr), and Last Glacial Maximum (LGM, 21 kyr). To verify whether AE were climatic stable since LGM we generated historical stability maps by overlapping presence/absence projections of all scenarios.

Results We identified two main AE corresponding to the southern and northern portion of the Espinhaço range suggesting a relatively strong latitudinal change in endemic anuran assemblages' composition. These areas, however, can be divided into six less inclusive operationally useful biogeographical units: (1) Quadrilátero Ferrífero, (2) Serra do Cipó, (3) Pico do Itambé, (4) Serra do Cabral, (5) Almas-Barbado, and (6) Serra do Sincorá. Areas of endemism are climatically different from each other ($p<0.001$) and their climatic similarity recovered well species composition similarities. Most AE are bounded by climatic barriers which correspond to the main landscape topographical discontinuities. Long-term stability areas were absent or small sized for most AE, besides Serra do Cipó which was predicted to have maintained most of its core area under stable climatic conditions since LGM.

Main conclusions Although the proposed AE and their relationships are consistent with previously postulated configurations, this study is the first dealing with a considerable number of vertebrate taxa to consider the entire range, revealing a more comprehensive and complex scenario than formerly recognized. We suggest that the observed pattern of endemism can be explained by a combination of current and historical climate, topography acting as geoclimatic barriers bounding AE, and numerical constraints (e.g. size, location and connection of sky islands). The potential presence of historical Atlantic forest refuges within lowlands valleys between southern and northern AE is suggested to have been acting as barriers since the LGM. Long-term climatic stability maps were congruent with current patterns of endemic species richness where Serra do Cipó is consistently recovered as areas of endemism for a variety of animal and plant endemic taxa, supporting the historical climate stability hypothesis. Palaeoclimate was also useful to recover historical connections between close related AE highlighting the potential important role played by Quaternary climatic fluctuations in shaping current

patterns of biodiversity. The identification of AE and the great endemic diversity they encompass have important implications for the conservation of high altitude Brazilian biota. The creation of new protected areas within AE is an imperative to meet a reserve system capable to ensure representation not only of the present anuran diversity, but also of the evolutionary processes that gave rise to it.

INTRODUCTION

Classifying areas into meaningful geographical units based on species distributions dates back to the early foundations of biogeography (e.g. Buffon, 1761; von Humboldt, 1806; de Candolle, 1855) but remains a central issue in modern biogeography (Kreft & Jetz, 2010). The delimitation of biogeographical units provides a basic summary of how species are distributed in space and constitutes the spatial framework for postulating hypotheses about the history of units and evolution of their biotas, the ultimate goal of the science of biogeography (Croizat et al., 1974; Rosen, 1978). The importance of well delimited spatially explicit units and robust systems classifying biogeographical patterns has been emphasized in recent years as they provide the basis for conservation planning (Olson et al., 2001; Whittaker et al., 2005; Mackey et al., 2008). However, the paucity of objective and replicable methods for identifying the units of biogeographical appraisals is still one of the major impediments within biogeography (Harold & Mooi, 1994).

Areas of endemism (AE) have been recognized as one of the most relevant and useful units in historical biogeography and remains an important tool for understanding the distribution of life on Earth (Crother and Murray, 2011). Non-random congruent distributional limits of geographically restricted taxa is the central idea behind the AE concept (Nelson & Platnick, 1981; Morrone, 1994; Linder, 2001). Because of their powerful operational value much emphasis has been placed on proposing methods of identifying AE operationally (e.g. Rosen, 1984; Morrone, 1994; Linder, 2001; Szumik et al., 2002; Szumik & Goloboff, 2004; Porzecanski & Cracraft, 2005; Deo & DeSalle, 2006), whereas the evolutionary processes involved in the formation of these units have been overlooked and remain poorly understood (Crother & Murray, 2011).

The corollary that the high level of species richness caused by aggregation of many small-ranged species, especially in montane regions, cannot be explained by models accounting solely for current climate variables has invited revamped research endeavor (Rahbek & Graves, 2001, Jetz & Rahbek, 2002, Jetz et al., 2004, Rahbek et al., 2007). As a consequence, efforts have started to take place to better integrate contemporary, evolutionary, and historical variables in an attempt to understand the variation in diversity and composition of biota among montane areas (Fjeldså et al., 2012). Among historical variables Quaternary stability in climate and vegetation, have proven to play an important role in shaping lineage diversification and biodiversity patterns in many tropical taxa (Hugall et al., 2002; Graham et al., 2006; Moritz et al., 2009; Carnaval et al., 2009). Areas of historical climate stability should allow more species to persist and speciate over time whereas extinction takes place in areas that experience the most severe climate changes, resulting in greater diversity in more stable areas (Ricklefs, 2006; Jablonski et al., 2006). Thus, AE may be expected to have experienced climatic stability allowing the aggregation of many small-ranged species trough time. This is particularly relevant from a conservation perspective because conservation action could focus on areas where lineages are expected to persist (because of low extinction rates).

Common biogeographical barriers can also result in spatial congruence in the distributions of species. Topographical features such as lowland valleys act as barriers to dispersal of highland taxa primarily because of the climatic challenges they impose on the physiology of organisms, especially in the tropics where organisms are expected to have narrow physiological tolerances to temperature (Janzen, 1967; Ghalambor et al., 2006). Reduced movements of organism across barriers should in turn lead to greater genetic divergence between populations, enhance allopatric speciation, and potentially result in greater species packing. Thus, barriers are also expected to play an important role in determining the existence and location of AE.

Because of their geographic isolation, notable latitudinal and altitudinal range, and high endemism, the greatest Brazilian mountain system, the Espinhaço range, provides an unusual opportunity to evaluate the role of barriers and Quaternary climatic oscillations on the delimitation of its AE. Rising at the crossroads between two neotropical hotspots (i.e. Atlantic Forest and Cerrado), and partially embedded in a semi-arid biome (Caatinga), the Espinhaço range (Figure 1) is the most extensive South American mountain range besides Andes and have played a key role in the diversification of the Neotropical high altitude biota (Giulietti et al., 1997). Constituted by at least eight large sky islands groups, extending about 1000 km across eastern Brazil, from a continental perspective, the Espinhaço can be considered a highland archipelago, because it is separated from other large blocks of South American highlands (Andes, Pantepui, and southern Brazilian ranges) by intervening lowland areas. As a result of altitudinal isolation, complex historical and ecological relationship with three Brazilian biomes, and great latitudinal variation, not only regional diversity is very high, but levels of endemism also are extraordinary (Harley, 1995; Giulietti & Pirani, 1988; Leite et al., in prep.).

We chose to analyse anuran species as study templates for the following reasons: Anura is the vertebrate order with the greatest number of endemic species in Espinhaço highlands. It has 47 endemic species of which many have very small range (< 500 km^2)

that aggregate in specific regions (Leite et al., in prep.). They are widely distributed in many different vegetation types, have high habitat and microhabitat fidelity, and contain an extensive variation in life-history traits (McDiarmid and Altig, 1999; Wells, 2007). Moreover, small range anurans are likely to have poor dispersal abilities and the historical effects on patterns of diversity have been hypothesized to be most important for low-dispersal taxa (Graham et al., 2006; Sandel et al., 2011). Additionally, the distribution of anuran endemic species, unlike other low-vagile vertebrate orders (i.e. Squamata), is relatively well known for the entire Espinhaço, thanks to a recent revision to be published by Leite et al. (in prep.). Hence, anuran species have the potential to serve as a model vertebrate group for studying animal distribution patterns and processes on tropical highlands, information critical for establishing conservation strategies based on evolutionary and biogeographical interpretations (Crisci, 2000). Our study was motivated by the urgent need to make progress with the detection of priority areas for conservation in the Espinhaço range, where a gap analysis demonstrated that 87% of the endemic frog species are not properly protected, one of the most worrying cases of species representation in reserves ever reported, considering gap analyses performed at different continents and various taxonomic groups (Leite et al., in prep.).

Here we use a combination of statistical classification methods, GIS mapping tools and palaeoclimatic modeling technics to provide a detailed and comprehensive biogeographical assessment of the Espinhaço AE. Our major goals are: (1) to identify AE for amphibian anurans in the Espinhaço range and explore their hierarchical relationships; (2) to investigate the role of topographical and climatic barriers in the delimitation of AE, and (3) to investigate the potential distribution of AE during the Quaternary climatic fluctuations determining if they were historically stable areas.

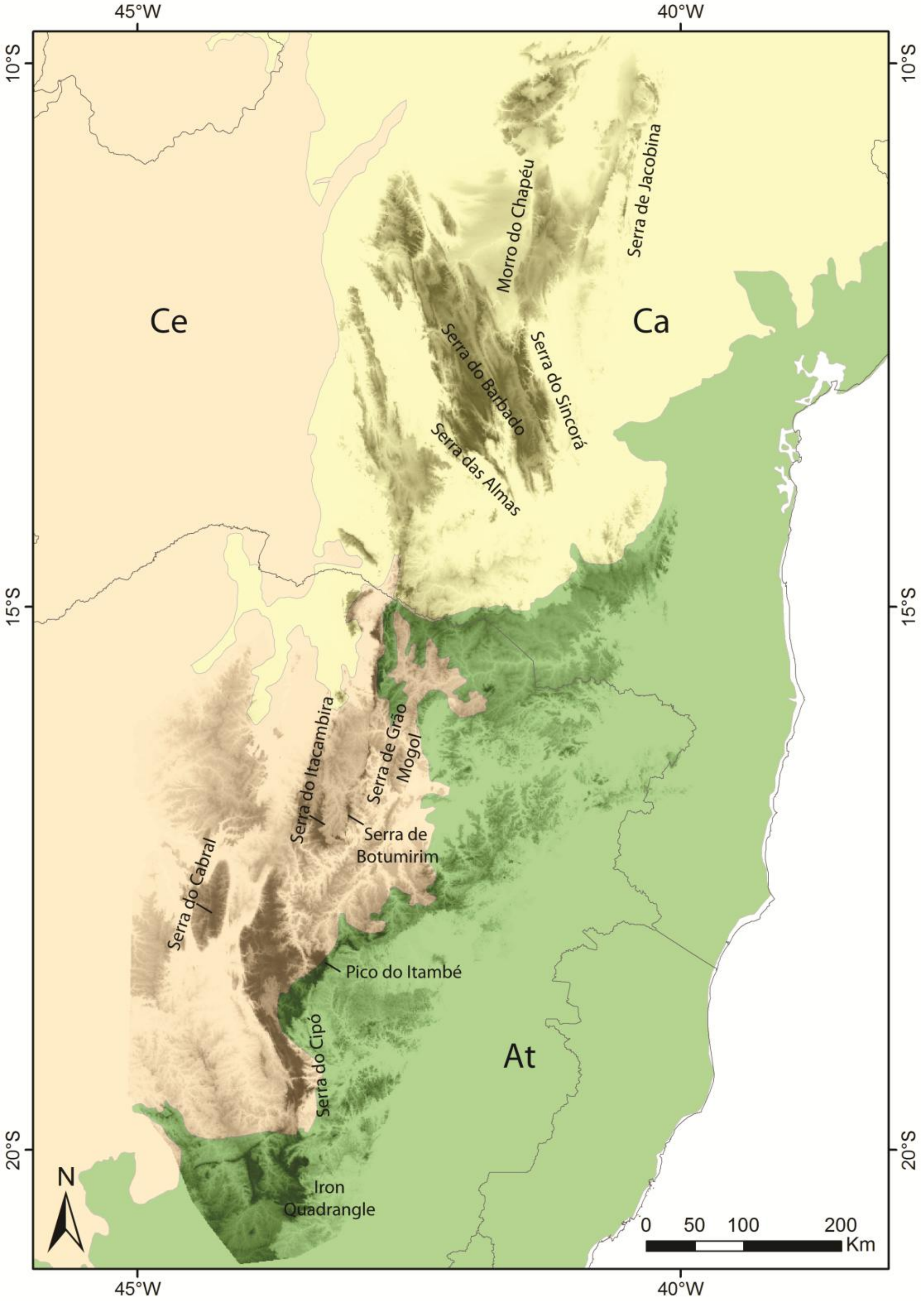

Figure 1 General location of the Espinhaço range in eastern Brazil, depicting main landscape features mentioned in the text and adjoining biomes: Atlantic forest (At), Cerrado (Ce), and Caatinga (Ca). Darker gray tones represent increasing elevations from 785 to 2072 m a. s. l. Gray lines indicate state limits.

METHODS

Selection of taxa

We performed our analyses with 47 anuran species currently recognized as Espinhaço endemics (Leite et al., in prep.). Of these, 13 (*c*. 28%) are undescribed taxa. All undescribed species considered in this study, however, represent easily diagnosable new taxa and many of them are in description process (Carvalho et al., in prep; Barata et al., in prep). Several other endemic species collected during the field work of this study were already described (Canedo et al., 2010; Leite et al., 2011; Leite et al., 2012), but unfortunately taxonomy work is not as fast as desired and time will still be need to describe all those taxa. Following Leite et al. (in prep.) we decided to use currently recognized unambiguously diagnosable new taxa as study units, in order not to waive the valuable biogeographic information they carry. On the other hand, some not easy diagnosable taxa were excluded from the analyses.

Distributional data

We obtained distributional data from careful physical examination of 17,240 voucher specimens (among which 5,096 regarded endemic species) housed in the most representatives Brazilian zoological collections (see the Acknowledgements). When available, we used geographical coordinates from museum databases, and in other instances, precise locations were obtained directly from collectors. When record coordinates were not available in museum databases, we approximated point localities from locality descriptions using Google Earth® and the Geoloc tool (available in http://splink.cria.org.br) to obtain these data as accurately as possible. To fill known sampling gaps (Leite et al., 2008) we conducted extensive fieldwork from 2007 to 2011 in 14 Espinhaço localities accounting for 140 days of fieldwork and 2021 georeferenced sampled anurans.

Identification of areas of endemism

We used the Geographic Interpolation of Endemism (GIE, Oliveira & Santos, in prep.) to identify and delimit AE along the Espinhaço range. GIE estimates the maximum overlay between the distributions of taxa through the interpolation of each species range centroid using a kernel density interpolator. For this, we calculated the centroid of the distribution of each species and measured the distance from this point to the furthermost point of their distribution. This distance was used as the area of influence (search radius) of the species centroids. Then, we classified species into six groups according to the size of their search radius (i.e. up to 61, 98, 189, 284, 394, and 751 Km) and generated one surface for each of these groups on which values are proportional to the density of species centroids. Finally, to build a multi-scale AE consensus map we reclassified all six maps, with kernel values varying between 0 and 1 and summed them. Areas with high kernel values were identified as AE. An itemized description of the method can be found in Oliveira & Santos (in prep.).

Areas of endemism relationships

To quantify compositional and climatic similarity among AE we performed cluster analyses using Jaccard’s and Euclidian distances, respectively, and unweighted pair-group method using arithmetic averages (UPGMA). To obtain the climatic dataset we extract values of the 19 bioclimatic variables available at the WorldClim database (Hijmans et al., 2005; http://www.worldclim.org/) to a resolution of 30″ (1 km^2) from 100 points randomly selected within each AE in altitudes above 1000 m of elevation.

This altitudinal threshold was applied because all endemic species occurs above it, despite a few could also be found below it.

To explore the ordination of climate within the entire study region, depicting sites of great climate variance, we performed a principal component analyses (PCA) on the 19 bioclimatic raster bands generating a single multiband raster, in which each band (shown by different colors) represents an axis. PCA was done in ArcGIS 10 (ESRI, Redlands, CA) using a covariance matrix after standardizing all variables by maximum values. To test if AE can be distinguished on the basis of their climatic conditions we conducted a canonical discriminant analysis using the four climatic variables related to precipitation and temperature used in the distribution models (see *Distribution modelling* section below for justification of use and list of variables).

Identification of environmental-climatic barriers

We used Monmonier's maximum difference algorithm (Monmonier, 1973) as implemented in BARRIER v. 2.2 (available at http: //www.mnhn.fr/mnhn/ecoanthropologie/software/barrier.html; Manni et al., 2004) to determine if AE are bounded by climatic breaks (i.e. areas where a given variable shows an abrupt rate of change) and if so, whether they coincide spatially with topographical discontinuities. Briefly, the Monmonier method connects all the samples (defined on a x, y coordinate system) with triangulations (Delaunay triangulation), then the distance measures (e.g. genetic, climatic, or something else) are associated with each edge of the triangulation, and a barrier is traced perpendicularly to those edges that have the maximum distances. The algorithm identifies boundaries from a distance matrix from specific localities. To build the distance matrices we used 100 randomly selected points for each AE and extract values of the 19 bioclimatic variables used in the analysis above, but considering a 20 km buffer in order to allow the identification of barriers between AE and non-AE. For a detailed description of the method see Manni et al. (2004).

Distribution modelling

To evaluate whether AE can be well predicted by our climate-based models and to determine if they were climatically stables areas we modelled the spatial range of each AE under current, Holocene and Last Glacial Maximum (LGM) projections. Current environmental-climatic variables were obtained from the same data sources at similar resolution than those used in the PCA analysis (see above). Past climate data for the Holocene (6 kyr bp) and the LGM (21 kyr bp) were derived from the ECHAM3 atmospheric general circulation model (DKRZ, 1992), available at the Palaeo-climatic Modelling Intercomparison Project webpage (PMIP; http://pmip.lsce.ipsl.fr/). From a set consisting of 19 bioclimatic variables relating to temperature and precipitation we included in the DMs only variables weakly correlated ($r < 0.8$) for the study area. This procedure was done to avoid or minimize overparameterization of our DMs with redundant variables. Therefore, current and past projections were carried out based on four climatic variables: temperature seasonality, temperature annual range, annual precipitation, and precipitation seasonality.

The occurrence datasets representing each AE were generated from 100 presence points randomly selected within their range, following the same procedure described for the PCA analysis (see above). We modeled current and palaeo distributions of AE using the Mahalanobis distance algorithm which measures the climatic similarity of each pixel to the mean of the available climatic space (Farber & Kadmon, 2003). This distance-based method was chosen due to its conceptual simplicity. Mahalanobis projections were implemented by the package openModeller Desktop 1.1.0 (http://openmodeller.sourceforge.net/). We converted models continuous outputs into presence/absence maps by applying the lowest presence threshold. To verify whether AE showed climatic stability we superimpose prediction maps obtained under current, 6 ka bp and 21 ka bp projections (Hugall et al., 2002; Carnaval & Moritz, 2008).

RESULTS

Identification of areas of endemism with GIE

We identified two broad-scale AE along the Espinhaço range here named Northern and Southern Espinhaço (NE and SE, hereafter; Fig. 2). The NE is entirely located in the State of Bahia ranging from Serra das Almas to Serra de Jacobina, including the Serra do Sincorá and the Morro do Chapéu, all of them important geographical designation of smaller mountains ranges. The SE corresponds to the ranges' portion within the state of Minas Gerais, from the Quadrilátero Ferrífero region, at its meridional portion, to mountains of bordering state of Bahia.

Areas of endemism are relative units depending on the scale they are observed (Platnick, 1992). Therefore, it is desirable to identify AE at different scales keeping their hierarchy (Crother & Murray, 2011). Accordingly, within the two more comprehensive AE above described we also defined six fine-scale areas with high kernel values (Fig. 2). The endemic species characterizing each AE are shown on Table 1. The NE had two very nearby AE located at southern portion of the Chapada Diamantina plateau, corresponding to the Serra das Almas, Serra do Barbado and other nearby ranges thus named the Almas-Barbado complex (Almas-Barbado); and the Serra do Sincorá (Sincorá) at the eastern slopes of Chapada Diamantina. The SE had four well geographically separated AE, with clear boundaries between them namely the

Quadrilátero Ferrífero located at the southernmost portion of the range; the Serra do Cipó (Cipó) which harbors the highest number of anuran endemic species; the Pico do Itambé (Itambé) corresponding to the highest summit of the Diamantina Plateau; and the Serra do Cabral (Cabral) an isolated mountain ridge located at the westerns slopes of the range (Fig. 2).

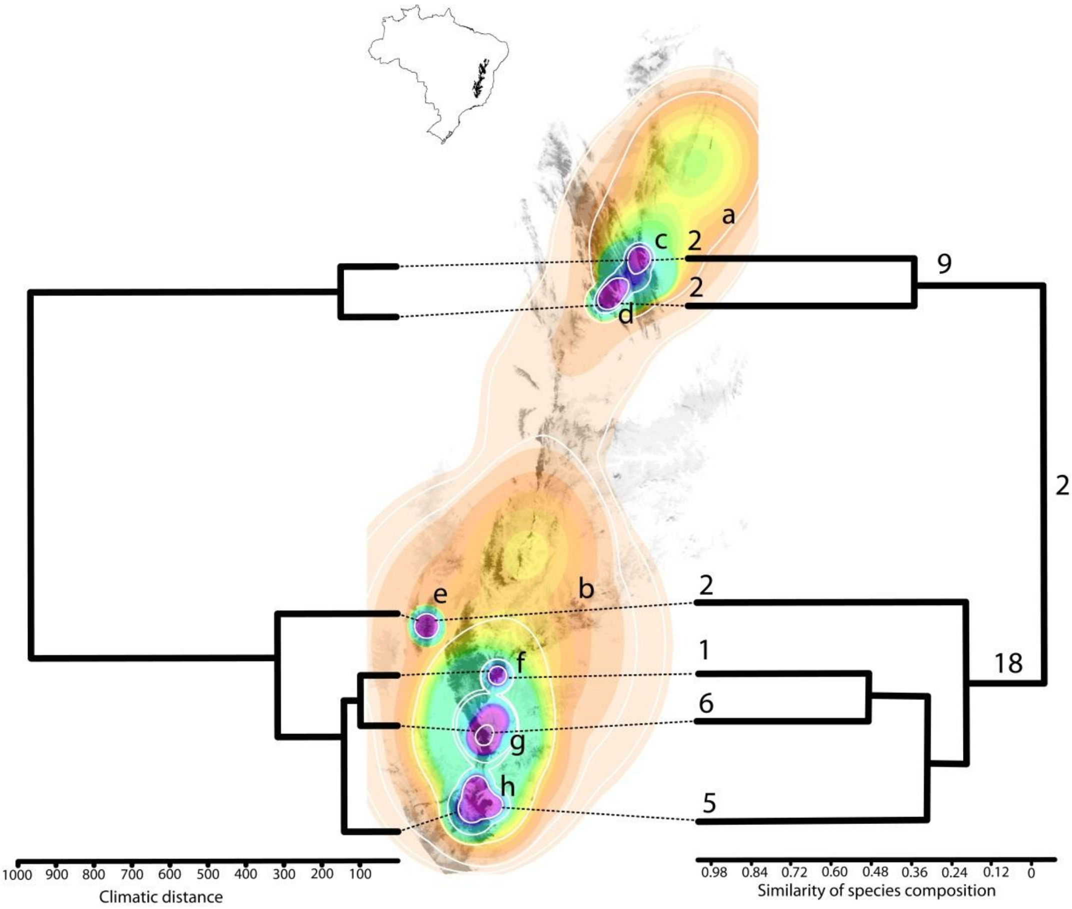

Figure 2 Areas of endemism (AE) for anurans in the Espinhaço range, Brazil, identified using Geographic Interpolation of Endemism analysis; based on groups of species with search radius of 61, 98, 189, 284, 394, and 751 Km. The white isolines define AE at multiple scales: (a) Northern Espinhaço; (b) Southern Espinhaço; (c) Serra do Sincorá; (d) Almas-Barbado complex; (e) Serra do Cabral; (f) Pico do Itambé; (g) Serra do Cipó; (h) Quadrilátero Ferrífero. Left: Dendrogram showing the climatic Jaccard's distance among AE. Right: Dendrogram showing the hierarchical clustering of AE regarding endemic species composition using Euclidian distance. Numbers show the number of exclusive species of each AE. Darker gray tones represent increasing elevations from 785 to 2072 m a. s. l.

Table 1 Espinhaço range endemic anuran species used in the Geographic Interpolation of Endemism analysis and their occurrence with areas of endemism. NE = Northern Espinhaço; SE = Southern Espinhaço; Almas-Barbado = Almas-Barbado complex; Sincorá = Serra do Sincorá; Cabral = Serra do Cabral; Cipó = Serra do Cipó; Itambé = Pico do Itambé. * indicates species exclusive to each fine-scale area of endemism. Species without * indicates species that occurs in an area of endemism but is not endemic to it.

Species	Area of endemism							
	NE	SE	Almas-Barbado	Sincorá	Cabral	Cipó	Itambé	Quadrilátero Ferrífero
Bokermannohyla diamantina	X	X	X					
Bokermannohyla flavopicta	X		X*					
Bokermannohyla oxente	X		X	X				
Pristimantis aff. *ramagii*	X		X	X				
Pristimantis sp.	X		X					
Pseudopaludicola aff. *mineira*	X		X*					
Scinax aff. *curicica*	X		X	X				
Scinax gr. *ruber*	X		X	X				
Strabomantis aramunha	X		X	X				
Bokermannohyla itapoty	X			X*				
Bokermannohyla juiju	X			X*				
Leptodactylus aff. *furnarius*	X		X	X				
Proceratophrys minuta	X			X				
Rupirana cardosoi	X			X				
Bokermannohyla sagarana		X			X*			
Scinax cabralensis		X			X*			
Aplastodiscus aff. *cavicola*		X				X*		
Bokermannohyla alvarengai		X				X	X	X
Bokermannohyla nanuzae		X				X	X	
Bokermannohyla saxicola		X			X	X	X	X

Crossodactylus trachystomus	X				X	X	X
Hylodes otavioi	X				X*		
Hypsiboas cipoensis	X				X*		
Leptodactylus camaquara	X				X	X	X
Phasmahyla jandaia	X				X		X
Phyllomedusa megacephala	X			X	X	X	
Physalaemus aff. *rupestris*	X				X*		
Physalaemus deimaticus	X				X*		
Physalaemus evangelistai	X				X	X	X
Physalaemus orophilus	X				X		X
Proceratophrys cururu	X				X	X	
Pseudopaludicola mineira	X			X	X	X	
Scinax curicica	X			X	X	X	X
Scinax gr. *catharinae*	X	X	X	X	X	X	
Scinax machadoi	X				X	X	X
Scinax pinima	X				X*		
Scinax tripui	X				X		X
Thoropa megatympanum	X			X	X	X	X
Crossodactylodes sp.	X					X*	
Hypsiboas botumirim	X					X	
Bokermannohyla aff. *feioi*	X						X*
Bokermannohyla martinsi	X						X*
Fritziana aff. *fissilis*	X						X*
Hylodes uai	X						X*
Physalaemus erythros	X						X
Sphaenorhynchus aff. *surdus*	X						X*
Pleurodema alium	X						

Areas of endemism relationships

The resulting dendrogram regarding species composition similarity retrieved a primary division between SE and NE areas of endemism, suggesting a relatively strong latitudinal change in endemic anuran assemblages' composition (Fig 2). Southern Espinhaço split in two main groups, one consisting of [Quadrilátero Ferrífero (Cipó, Itambé)] and other by Cabral. Dendrograms showing the clustering of AE accordingly to climate variables recovered the same topology found by clustering areas accordingly to species composition (Fig 2).

The SE and NE were located at the opposite extremes of the climatic gradient (Fig. 3). The first axis explained 59% of the variance and distinguished regions with higher values of annual precipitation, precipitation of wettest month, precipitation of wettest quarter, and precipitation of warmest quarter (represented by blue tones, i.e. southern AE) from areas with dryer climates (darker tones, i.e. northern AE; Fig. 3 & Tab. 2). The second axis explained 29% of the variance adding to 88% of cumulative variance in the two first axes. The most important attributes to this component with positive loadings was the precipitation seasonality and with negative loadings the precipitation of driest month and precipitation of coldest quarter (Fig. 3 & Tab. 2). The third axis explained 5% of the variance and discerned regions with higher values of year round mean temperatures (represented by red tones which corresponds to lowlands) from cooler regions (darker tones). This component illustrates the inverse effect of elevation on temperatures and recovered well the topography of the Espinhaço. The composite map showing the first three axes overlaid shows how Espinhaço climate is heterogeneous (Fig. 3).

We found significant differences among AE regarding its climate variables (Wilk's λ=0.0001; F 20, 2140=1233.3; p<0,001; Fig. 4) being all of them different from each other (p<0,001). All four variables used contributed to the discriminant model being the most useful in a decreasing order: annual precipitation (F-value = 989.7; tolerance = 0.425), temperature seasonality (F-value = 542.5; tolerance = 0.717), precipitation seasonality (F-value = 323.2; tolerance = 0.402), and temperature annual range (F-value = 307.6; tolerance = 0.349). The discriminant function correctly classified 95.3% of the cases.

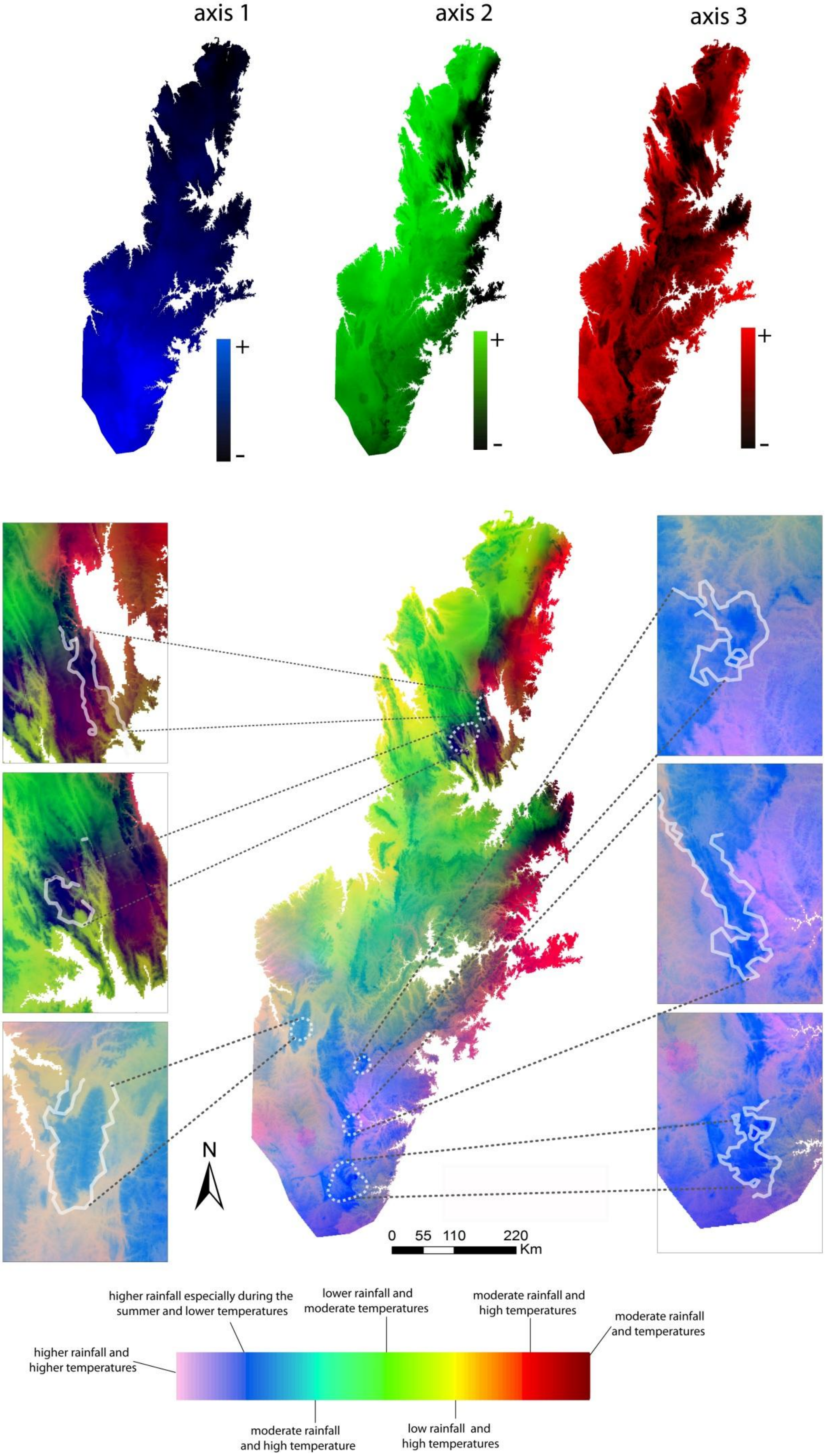

Figure 3 Map representing the first three principal components of the climatic space of the Espinhaço range, eastern Brazil. In the first axis blue tones distinguish regions with higher annual precipitation from areas with dryer climates, especially during the summer (darker tones). In the second axis green tones distinguish areas with greater precipitation seasonality from areas with higher precipitation in the coldest and dryer season. In the third axis red tones distinguish regions with higher year round mean temperatures from cooler regions. White dashed lines represent areas of endemism. Solid white lines presented in each zoom show the results from the Barrier analysis indicating climatic breaks.

Table 2 Contribution of the 19 bioclimatic variables for the first three PCA axes, calculated for the entire Espinhaço range, eastern Brazil. Values smaller than − 0.3 and greater than 0.3 are only denoted by positive or negative signs.

		PCA axes		
		1	2	3
Variable	Description			
BIO1	Annual mean temperature	-	+	0.35
BIO2	Mean diurnal range	+	+	+
BIO3	Isothermality	-	+	-
BIO4	Temperature seasonality	+	-	+
BIO5	Max temperature of warmest month	-	+	+
BIO6	Min temperature of coldest month	-	+	+
BIO7	Temperature annual range	+	+	+
BIO8	Mean temperature of wettest quarter	-	+	0.35
BIO9	Mean temperature of driest quarter	-	+	0.36
BIO10	Mean temperature of warmest quarter	-	+	0.35
BIO11	Mean temperature of coldest quarter	-	+	0.35
BIO12	Annual precipitation	0.41	-	+
BIO13	Precipitation of wettest month	0.45	+	+
BIO14	Precipitation of driest month	-	-0.47	+
BIO15	Precipitation seasonality	+	0.45	-
BIO16	Precipitation of wettest quarter	0.48	+	+
BIO17	Precipitation of driest quarter	-	-0.37	+
BIO18	Precipitation of warmest quarter	0.45	-	+
BIO19	Precipitation of coldest quarter	-	-0.56	+
Variance explained (%)		59	29	5
Eigenvalues		0.06	0.03	0.01

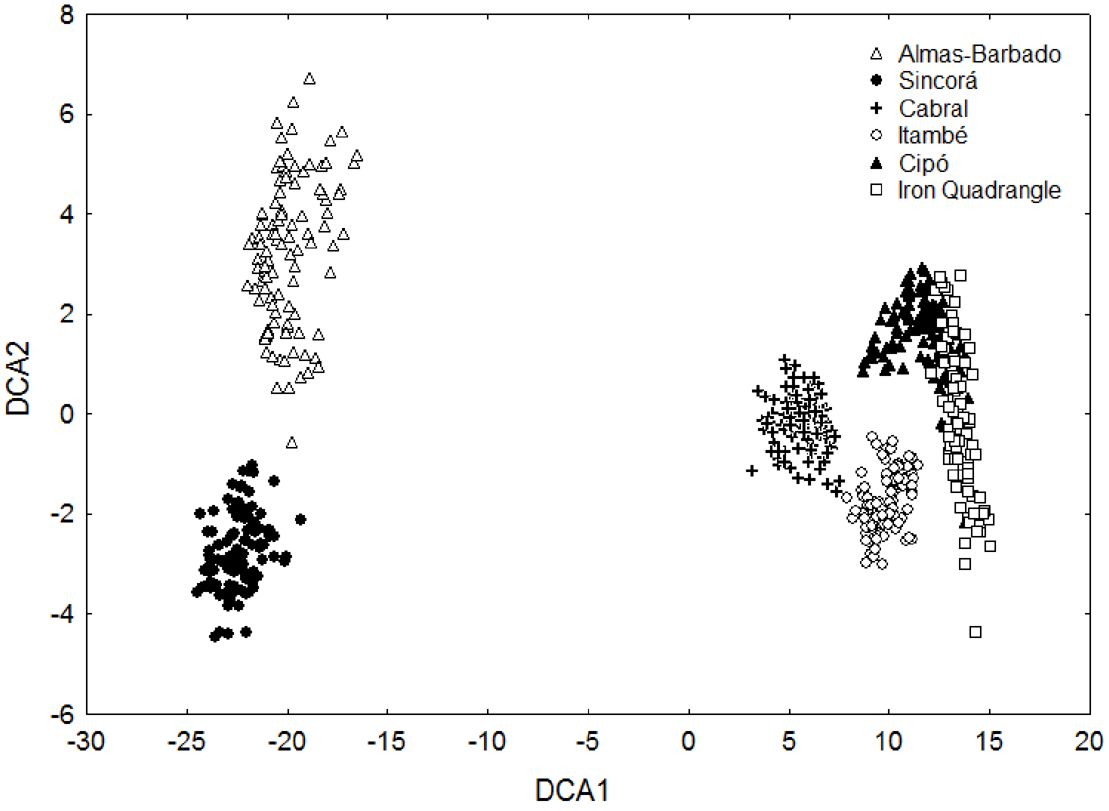

Figure 4 Representation of the first two axis of the canonical discriminant analysis for the environmental variables extracted from point comprised within the six fine-scales anuran areas of endemism of the Espinhaço range, eastern Brazil.

Identification of environmental-climatic barriers

All four southern fine-scale AE and Sincorá at northern Espinhaço were found to have clear climatic barriers limiting their distribution (Fig. 3). These climatic breaks were largely congruent with major landscape topographical discontinuities (i.e. high steep slopes with great altitudinal range) which were found to recover well the climatic variation within the Espinhaço (Fig. 3). BARRIER analysis did not outline completely the Almas-Barbado AE. However, the strongest climatic breaks found within this area were still largely coincident with elevational-climatic discontinuities as it outlined the Barbado massif, which has the highests summit of the northern Espinhaço (Fig. 3).

Distribution modeling and historical stability

Current climatic conditions were good predictors of AE distribution (Fig. 5). Nevertheless, our model slightly over-predicted Quadrilátero Ferrífero and Cipó distribution northwards (Fig. 5e-f). There were also minor over-predictions of the Itambé and Cabral distributions, but all of them consisted in small disjoint areas with low similarity values (Fig. 5d-e). The projections for all AE climatic conditions under the Holocene scenario revealed to be similar to the predictions made for the current climate and more widespread than at the LGM climatic scenario, except for the Itambé and Quadrilátero Ferrífero which were found to be more widespread at the LGM than at the Holocene (Fig. 6). Quadrilátero Ferrífero, Cipó and Itambé current climatic connections were predicted to have persisted since the Holocene (Fig. 5 d-f). However, during the LGM estimated palaeomodelling depicts a break between the distribution of Quadrilátero Ferrífero and Cipó, whereas Itambé remained connected with Cipó (Fig. 5d-f). Climatic connections were not predicted to have occurred between Almas-Barbado and Sincorá since LGM, besides a tenuous climatic bridge established between them at the Holocene (Fig. 5a-b).

Areas consistently predicted under current, 6 ka bp and 21 ka bp projections and therefore considered of long-term stability where found in all AE, except for Cabral and Almas-Barbado for which current climatic conditions were not predicted to occur within their boundaries under the LGM scenario (Fig. 6). However, long-term stability areas were few and small sized within Sincorá, Itambé and Quadrilátero Ferrífero. Interestingly, the small refugium predicted within Itambé corresponds precisely to the Itambé summit, the highest mountain of that region reaching 2044 m a. s. l. Conversely, Cipó was predicted to have maintained most of its core area under stable climatic conditions since the LGM.

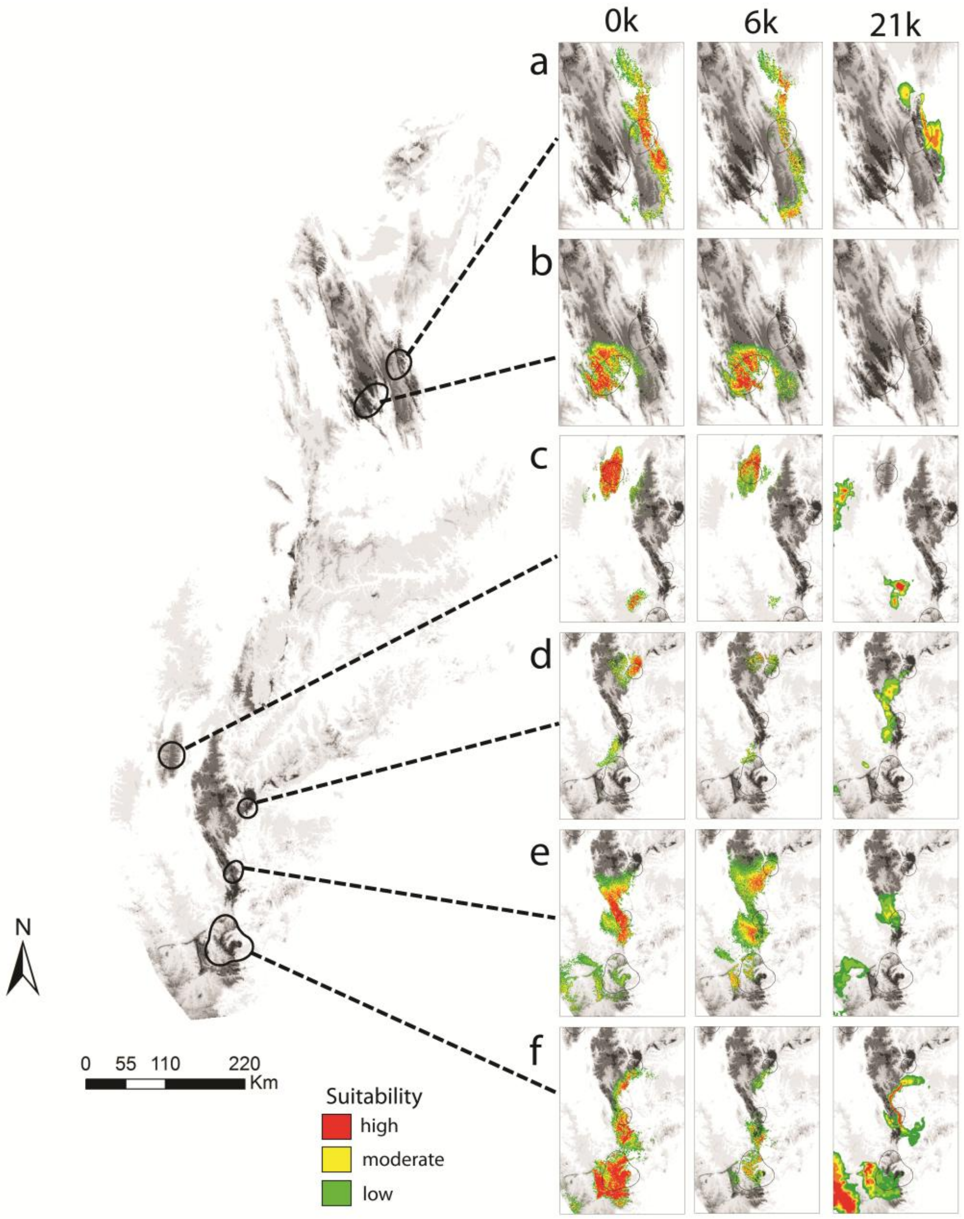

Figure 5 Modelled ranges of the Espinhaço range areas of endemism (AE) for the Last Glacial Maximum (LGM, 21 ka), the mid-Holocene (6 ka), and current climatic scenarios. Darker lines represent the limits of each AE: (a) Serra do Sincorá, (b) Almas-Barbado complex, (c) Serra do Cabral, (d) Pico do Itambé, (e) Serra do Cipó, and (f) Quadrilátero Ferrífero areas of endemism. Darker gray tones represent increasing elevations from 785 to 2072 m a. s. l.

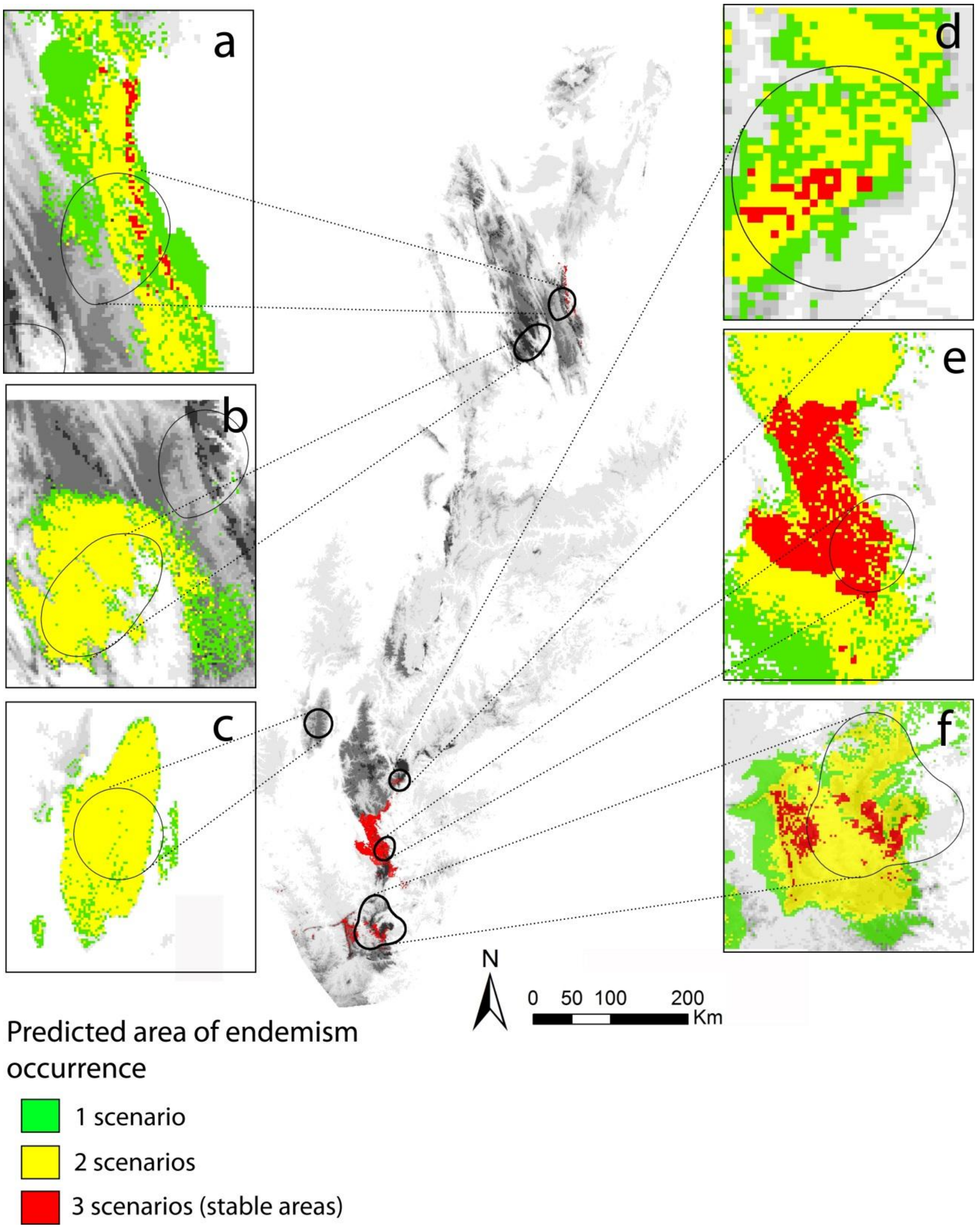

Figure 6 Espinhaço range areas of endemism historical stability surfaces obtained by overlapping across predicted logistic outputs under current, 6 ka and 21 ka climatic scenarios. (a) Serra do Sincorá, (b) Almas-Barbado complex, (c) Serra do Cabral, (d) Pico do Itambé, (e) Serra do Cipó, and (f) Quadrilátero Ferrífero areas of endemism. Darker gray tones represent increasing elevations from 785 to 2072 m a. s. l.

DISCUSSION

Espinhaço areas of endemism

There are few published maps of endemism either in Espinhaço fauna and flora, making comparisons with other taxa groups problematic, stressing the relevancy of the results provided herein. There is only one study with vertebrate species (birds) aiming to determine AE along the Espinhaço range which identified areas in total accordance with ours SE and NE macro-areas (Vasconcelos, 2008; Vasconcelos et al., 2008). However, the small number of Espinhaço endemic birds analyzed (four) and their wider distribution within the range, if compared to those of anurans, allowed the delimitation of only broad-scale AE (Vasconcelos, 2008; Vasconcelos et al., 2008). Conversely, the more diverse anuran fauna with species ranging from relative wide-spread to narrowly endemic enable us to break these previously macro-areas in six less inclusive, functional and operationally useful biogeographical units.

Furthermore, there are only two other attempts to identify AE within the Espinhaço range which dealt with a considerable number of species (i.e. Echternacht et al., 2011; Ribeiro et al., 2012). Both appraisals dealt with endemic plant taxa, but the former was restricted to the southern portion of the range whereas the latter covered the entire Espinhaço. Echternacht et al. (2011) and Ribeiro et al. (2012) major findings are largely coincident with the AE identified in our study. Both of them also identified the Quadrilátero Ferrífero, Cipó, Itambé (being part of their Diamantina Plateau), and Cabral as AE. On the other hand, Echternacht et al. (2011) did not considered the southern Espinhaço (the ranges' portion within Minas Gerais) as an area of endemism as a whole, because none of the species they analyzed occurs throughout the entire region. Conversely, we found SE should be considered an AE, sharing at least six endemic species throughout its entire range (*B. alvarengai*, *B. saxicola*, *P. megacephala*, *L. camaquara*, *C. trachystomus*, and *T. megatympanun*), a pattern also verified for the endemic Hyacinth Visorbearer *Augastes scutatus* (Vasconcelos, 2008) as well for plant taxa such as the Cactaceae *Cipocereus minensis* (Zappi & Taylor, 2008). This result suggests Echternacht et al. (2011) finding could be due to a sampling bias as they included only selected (but representative) taxa in their analysis. Nevertheless, species occurring through the whole SE seems not to be a common pattern within endemic plants.

Within NE Ribeiro et al. (2012) delimited an AE they named Rio de Contas which corresponds to our Almas-Barbado, based on the occurrence of two microendemic *Minaria* (Apocynaceae) species. However, they were unable to identify our Sincorá as AE because it harbors no exclusive endemic species. Here we propose NE should be divided in two AE, the Almas-Barbado and the Sincorá. Although the novelty behind this assertion, floristic dissimilarities among these blocks are already well documented (Harley, 1995; Zappi et al., 2003) and we expect similar findings should be achieved if a proper methodological approach regarding the delimitation of AE using a larger species data set is applied.

These agreements indicate that anuran AE have significant generality, because endemic frogs along the Espinhaço range tend to cluster in the same regions as other groups, including plants and birds. Thus, patterns that emerge from this analysis might be extrapolated for other groups of organisms in Espinhaço. Accordingly, this generality implies that anurans could be considered not as only good models for the studies of speciation and evolution of high altitude tropical biota, but as well as surrogates groups for the field of biogeography conservation.

Area of endemism relationships

The area dendrogram accounting for species composition similarity recovered well climatic similarities between AE. The faunistic segregation between the SE and NE is evident as well their climatic conditions. The SE is cooler and more humid than NE. The higher temperatures of the NE are affected not only by its lower latitude but by its location within a semi-arid biome (Caatinga), which also contributes to dry the climate. On the other hand, the lower latitudes and the stronger Atlantic Forest influence, especially at the eastern slopes of its southern portion (Ribeiro et al., 2009), make the SE climate more amenable and mesic than that of NE. The influence of biomes has been suggested to play a central role in the distribution of taxa in this ecotonal mountain range (e.g. Rapini et al., 2002; Zappi et al., 2003; Kamino et al., 2008). Despite their low similarity (only two shared endemics) SE and NE relationships may be accessed on an infra-specific level. The occurrence of distinct but closely related species (i.e. *Bokermannohyla alvarengai* / *B. itapoty* and *B. saxicola* / *B. oxente* (Lugli & Haddad, 2006a; 2006b) with disjunct distributions in the SE and NE, respectively, suggests the existence of a historical connection between these areas (Leite et al., 2008). The same distribution pattern is also found for the pair of hummingbirds *Augastes scutatus* and *A. lumachella* (Vasconcelos, 2008), reinforcing the phylogenetic proximity between SE and NE Espinhaço biotas.

Within SE, the Cipó and Itambé were clustered together regarding compositional and climate similarities. In fact, these areas share the largest number of species among all other AE and the pair of close related species *Hypsiboas cipoensis* / *H. botumirim*. Furthermore, palaeomodelling predicted these AE to be climatically connected since the

LGM, whereas current and past connections with the Quadrilátero Ferrífero were predicted to be weak and persisted only since Holocene. Moreover, Cipó and Itambé constitute the largest continuous topographic island above 1000 m of elevation within SE which in turn is separated from the Quadrilátero Ferrífero by originally forested lowland valleys suggesting besides current and historical climatic resemblance altitudinal connectivity may also play an important role in shaping current patterns of distribution of endemic species. In addition, Cipó and Itambé share the same geological origin and both rely on quartizitic soils whereas the Quadrilátero Ferrífero soils are mainly ferruginous (Almeida-Abreu, 1995; Gontijo, 2008; Renger et al., 1994). Specific soil types may affect not only vegetation but the availability of different types of water bodies (e.g. permanent streams rarely occur in iron ore soils) which in turn are expected to affect anuran species composition. The existence of an endemism unit formed by Cipó and Itambé is also corroborated by the works of Echternacht et al. (2011a, 2011b). Conversely, the Cabral is the Espinhaço most western ridge, the only AE fully located within the Cerrado biome, and was not predicted to have established climatic condition with any nearby AE since LGM. Not surprisingly, it is the most dissimilar AE within SE, both climatically and regarding species composition.

We provide evidence that the pattern of AE clustering may be explained by a combination of current climate similarity, Quaternary climatic connections, topographic connection and geomorphology resemblance. Because current clustering of AE can reflect just patterns of ecological similarities among units instead of historical patterns (Brooks and van Veller, 2003), our results should be interpreted with caution. The AE relationships hypothesis proposed here needs to be specifically addressed by multiple lineages comparative molecular phylogenetic/phylogeographic methods of Espinhaço endemic taxa.

Climate, barriers and areas of endemism

We found fine-scale AE are outlined by geoclimatic barriers (i.e. climatic brakes corresponding to main topographical discontinuities) which are likely to prevent individuals from colonizing nearby isolated environmental suitable islands promoting allopatric speciation and potentially resulting in spatial congruence in the distributions of species. This should be especially relevant for low-vagile organism such as anurans. It is worth nothing that the highest summits within AE Quadrilátero Ferrífero, Itambé and Almas-Barbado are outlined by strong geoclimatic barriers. Not by chance, Espinhaço summits harbor some micro-endemic frogs such as the highly specialized bromeligenous (*sensu* Peixoto, 1995) frogs *Crossodactylodes* sp. and *Fritziana* aff. *fisilis* restricted to one or two mountain tops in the Itambé and Quadrilátero Ferrífero, respectively, and *Bokermannohyla flavopitca* from the Almas-Barbado, all of them restricted to elevations above 1600 m a. s. l. (Leite et al., 2012; F.S.F.L. pers. obs.).

On the other hand, if species can reach all areas environmentally suitable for colonization (no barrier effect) spatial patterns of endemism could be driven purely by environmental variables, especially in regions with heterogeneous climate. We found Espinhaço AE are very different climatically from each other suggesting besides the barrier effect, the current climatic gradient could be acting as an environmental filter preventing species from adapting to different novel environments and therefore could also be playing an important role in explaining the occurrence of AE exclusive taxa (Ricklefs, 2006).

Unlike fine-scale AE which are well bounded by clear geoclimatic barriers we suggest the broad-scale areas are delimited by taxon-specific barriers, as the distributions of endemic species that defines both these areas are not totally congruent. Thus, we propose the large region corresponding to the northern state of Minas Gerais and bordering Bahia (and the climatic space comprised within it) constitutes a composite barrier between SE and NE. Moreover, paleoclimate modeling infers this region between SE and NE was a historically stable area for Atlantic forest (under broader definition) since the LGM (see Fig. 3 of Carnaval & Moritz, 2008). Forested environments are possibly a strong barrier for high altitude species most of them open-field dwellers or inhabiting narrow riverine forests that grows along small mountain streams. The presence of dense forests within valleys would have hampered dispersion between the small and already isolated by distance sky islands of northern Minas Gerais. This long-term isolation hypothesis is supported by the pre-Pleistocene (4-3,5 million years before present) divergence times of the major clades of the SE endemic anuran *Bokermannohyla saxicola* currently inhabiting sky islands of northern Minas Gerais, Cabral, Itambé and Cipó (A. C. A. Nascimento, unpublished data).

The location of this barrier is somewhat congruent with the climatic break identified between areas of endemism for spiders in the Atlantic forest (Oliveira & Santos, in prep.), which in turn coincide with the division of areas of endemism of birds (Silva et al., 2004) and areas of endemism richness of butterflies (Tyler et al., 1994) and bamboos (Soderstrom et al., 1988), all of them located nearby the Doce river. These congruent patterns suggests that besides regional factors (i.e. geoclimatic barriers), there seems to be enviromental-climatic factors at continental scales affecting Espinhaço endemic anurans distribution.

Areas of endemism and historical stability

Quaternary climate stability has been showed to explain diversity patterns in temperate (Araújo et al., 2008) and distinct tropical regions of the world (Hugall et al., 2002; Graham et al., 2006) including the Brazilian Atlantic forest and Cerrado (Carnaval & Moritz, 2008; Werneck et al., 2012). We show that palaeoclimate also has predictive value relative to spatial patterns of species diversity in Brazilian high altitude regions with complex topography and steep environmental gradients. The only AE predicted to have maintained most of its area under stable climatic conditions since the LGM was the Cipó. This prediction is in accordance with the patterns of species richness found across the Espinhaço in which Serra do Cipó is consistently recovered the richest area for a variety of animal and plant endemic taxa (Echternacht et al., 2011; Ribeiro et al., 2012, Versieux & Wendt, 2007, Vasconcelos & Rodrigues, 2010 and Freitas et al., 2012), including amphibians (Leite et al., in prep.).

This study provides evidence that differential impacts of Quaternary climate oscillation associated with environmental heterogeneity have shaped the distribution patterns of endemic anuran species in the Brazilian highlands. The prediction that refugial areas should harbor higher genetic diversity (Hugall et al., 2002; Carnaval et al., 2009) deserves further testing and comparative phylogeographic studies regarding low-dispersal high altitude endemics organisms appear as good templates for answering this question.

Conservation remarks

The patterns of diversification and regional differentiation described here have important implications for conserving the extraordinary Espinhaço biodiversity. Espinhaço AE are of great significance for conservation as they define regions that collectively contain both a large percentage of biodiversity and have taxa not likely to occur in many other areas. The delimitation of several areas of endemism within the most extensive Brazilian mountain range suggests that small areas are especially involved in contributing to its entire biodiversity. Fortunately, five out of six Espinhaço AE are represented by strictly protected reserves (IUCN categories I to III). However, current reserve system is definitely not well located or large enough as Leite et al. (in prep.) reported for Espinhaço endemic anurans one of the most worrying cases of species representation in protected areas ever reported, considering gap analyses performed at different continents and various taxonomic groups. The creation of new reserves and the enlargement of the already established within Espinhaço AE are imperatives to meet a protected area system capable to ensure representation not only of the present anuran endemism diversity, but also of the evolutionary processes that gave rise to it.

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Capítulos 3 e 4 (Publicados)

Capítulo 3

Leite *et al.* 2011. A new species of *Bokermannohyla* from the Espinhaço range, state of Minas Gerais, Southeastern Brazil. Herpetologica **67:**440–448.

Capítulo 4

Leite *et al.* 2012. A new species of the *Bokermannohyla pseudopseudis* group from the Espinhaço range, central Bahia, Brazil (Anura: Hylidae). Herpetologica **68:** 401–409.

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A NEW SPECIES OF *BOKERMANNOHYLA* FROM THE ESPINHAÇO RANGE, STATE OF MINAS GERAIS, SOUTHEASTERN BRAZIL

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Abstract: A new species of the *Bokermannohyla pseudopseudis* group similar to *B. alvarengai* and *B. itapoty* is described from Serra do Cabral, Espinhaço Range, Minas Gerais, southeastern Brazil. It is diagnosed by having a medium size (male 47.3–54.8 mm; female 44.5–48.6 mm); short snout, truncate in lateral and dorsal views; head 1.01–1.07 times wider than long; tympanum 0.08–0.09 times snout–vent length (SVL); hypertrophied forearm; well-developed prepollex; nuptial pad small, with two separate areas covered with small keratinized spiculae, on medial and lateral edge of the base of the prepollex; dorsal color pattern composed of dark gray blotches of irregular shape on a light gray background, without a central light spot, resembling lichens incrusted on rocks; dark gray perpendicular bars covering the whole dorsal surface of thighs, rarely branched, without light spots, highly contrasted with the background color; and the lack of a white stripe over the vent.

Key words: Amphibia; *Bokermannohyla pseudopseudis* species group; *Bokermannohyla sagarana*; Endemism; New species; Taxonomy

On the basis of a phylogenetic analysis based mostly on molecular data, Faivovich et al. (2005) erected *Bokermannohyla* to accommodate the former *Hyla circumdata*, *H. claresignata*, *H. martinsi*, and *H. pseudopseudis* species groups. The genus occurs only in the Brazilian Atlantic Forest, Cerrado and Caatinga biomes and currently comprises 29 species. The *Bokermannohyla pseudopseudis* species group was first suggested by Pombal and Caramaschi (1995) to allocate *B. pseudopseudis* and *B. saxicola*. It was formerly recognized by Caramaschi et al. (2001), in which *B. ibitiguara* was removed from the *B. circumdata* species group to the *B. pseudopseudis* species group. Faivovich et al. (2005) recognized a *B. pseudopseudis* species group including *B. alvarengai*, *B. ibitiguara*, *B. pseudopseudis*, and *B. saxicola*. Subsequently, Lugli and Haddad (2006*a*) proposed the *B. alvarengai* species group to allocate *B. alvarengai* and *B. itapoty*, based on their similar morphological and behavioral characteristics. Faivovich et al. (2009) argued that as there are no known synapomorphies for the remaining species of the *B. pseudopseudis* group (*B. ibitiguara*, *B. oxente*, *B. pseudopseudis*, and *B. saxicola*) and that a *B. alvarengai* species group has the potential of making the *B. pseudopseudis* species group paraphyletic. Therefore, we prefer to recognize the *B. pseudopseudis* species group as proposed by Faivovich et al. (2009) containing all species included by Faivovich et al. (2005) and Lugli and Haddad (2006*b*) plus *B. itapoty*.

The *B. pseudopseudis* species group is distributed in mountains of the Espinhaço Range in the States of Minas Gerais (*B. alvarengai* and *B. saxicola*) and Bahia (*B. itapoty* and *B. oxente*), Serra da Canastra in the State of Minas Gerais (*B. ibitiguara*), and Planalto Central in the State of Goiás and Federal District (Brasília; *B. pseudopseudis*), Brazil. During fieldwork in the Serra do Cabral, a regional designation of the Espinhaço Range, State of Minas Gerais, southeastern Brazil, we collected specimens of a new species of *Bokermannohyla* similar to *B. alvarengai* and *B. itapoty*. The new species is described herein.

Materials and Methods

Specimens used in the description or examined for comparisons are deposited in the following Brazilian institutions: UFMG (Universidade Federal de Minas Gerais, Belo Horizonte, Minas Gerais), MZUFV (Museu

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de História Natural João Moojen, Universidade Federal de Viçosa, Viçosa, Minas Gerais), LZV (Laboratório de Zoologia dos Vertebrados, Universidade Federal de Ouro Preto, Ouro Preto, Minas Gerais), and MNRJ (Museu Nacional, Rio de Janeiro, Rio de Janeiro). Webbing formula notation follows Savage and Heyer (1967), as modified by Myers and Duellman (1982). Measurements of adult specimens were taken with a Mytutoyo digital caliper to the nearest 0.01 mm, and follow Duellman (1970), with the exception of thigh length. Abbreviations used in the measurements are SVL (snout–vent length), HL (head length), HW (head width), ED (eye diameter), TD (tympanum diameter), IOD (interorbital distance), END (eye–nostril distance), IND (internarial distance), THL (thigh length), TBL (tibia length), and FL (foot length, excluding tarsus length, following Duellman, 1970). Characters used for species comparisons were taken from Bokermann (1956), Lugli and Haddad (2006*a*), Sazima and Bokermann (1977) for *B. alvarengai*; Bokermann (1956), Lugli and Haddad (2006*b*), Pombal and Caramaschi (1995) for *B. saxicola*; Lugli and Haddad (2006*b*), Pombal and Caramaschi (1995) for *B. pseudopseudis*; Cardoso (1983), Lugli and Haddad (2006*b*) for *B. ibitiguara*; Lugli and Haddad (2006*a*) for *B. itapoty*; Lugli and Haddad (2006*b*) for *B. oxente*, and from specimens listed in Appendix I. Morphometric features from literature were often not available as individual measurements; sometimes showing only average values, a range or a nonspecific sample size (*n*). In these cases measurements were presented as range (min–max) and ratios were calculated by dividing average values and therefore they are shown without range or sample size. Sex was determined by presence or absence of secondary sexual characters (forearm hypertrophy, prepollical spine, vocal slits). The datum used for geographic coordinates was WGS84.

SPECIES DESCRIPTION

Bokermannohyla **sagarana** *sp. nov.*

(Figs. 1–3, Table 1)

Holotype.—UFMG 4246, adult male, 16 December 2007, Serra do Cabral (17°40′37,4″S, 44°20′20,4″W, 1185 m above sea level), Municipality of Joaquim Felício, State of Minas Gerais, Brazil, T. L. Pezzuti and L. O. Drummond (Figs. 1, 2, 4B).

Paratopotypes.—UFMG 4238, adult male, 17°42′15.2″S, 44°17′50.3″W, 1180 m above sea level (Fig. 3). UFMG 4240–41, adult females; UFMG 4239; 4242–4245, adult males, 17°41′23″S, 44°17′13.1″W, 1185 m elevation. All collected by T. L. Pezzuti and L. O. Drummond on 16 December 2007.

Paratypes.—UFMG8614–19, adult males, 08 December 2010, 17°53′30.6″S, 44°17′50″W, 1225 m above sea level; UFMG8620–21, adult males, 10 December 2010, 17°51′46.8″S, 44°17′49.2″W, 1222 m above sea level. All collected at Fazenda Bimbarra, Serra do Cabral, Municipality of Buenópolis, State of Minas Gerais, Brazil, L. O. Drummond and A. J. R. Cruz.

Diagnosis.—The dorsal color pattern composed by dark gray blotches in a light gray background, resembling to lichens encrusted on rocks, distinguishes *B. sagarana* (Fig. 1A) from all species of the *B. circumdata* group, which have brown dorsum, and from all species of the *B. claresignata* group, which have yellow to beige dorsum. The absence of a ventral humeral crest developed as a spine in males promptly distinguishes *B. sagarana* from all species of the *B. martinsi* group.

Individuals of *B. sagarana* (male SVL 47.3–54.8 mm, $n = 7$; female SVL 44.5–48.6 mm, $n = 2$; Table 1) are much smaller than *B. alvarengai* (male SVL 60.7–140.9 mm; female SVL 78–87.6 mm); males of *B. sagarana* are larger than males of *B. itapoty* (SVL 37.8–46.3 mm, $n = 12$) and *B. oxente* (SVL 38.8–43.4 mm, $n = 14$). *Bokermannohyla sagarana* have heads 1.01–1.07 ($n = 9$) times wider than long (Table 1), as the remaining species of the *B. pseudopseudis* group, with the exception of *B. oxente* and *B. saxicola*, in which the heads are as long as wide (1.0 times wider than long; based on the average measures of 14 male specimens; Lugli and Haddad, 2006*b*) and 1.14 longer than wide (based on average measures of 13 male specimens; Pombal and Caramaschi, 1995), respectively. The new species has a larger tympanum (TD/SVL 0.08–0.09; $n = 9$) than *B. itapoty* (TD/SVL 0.06; based on the average measures of 12 male specimens; Lugli and Haddad, 2006*a*)

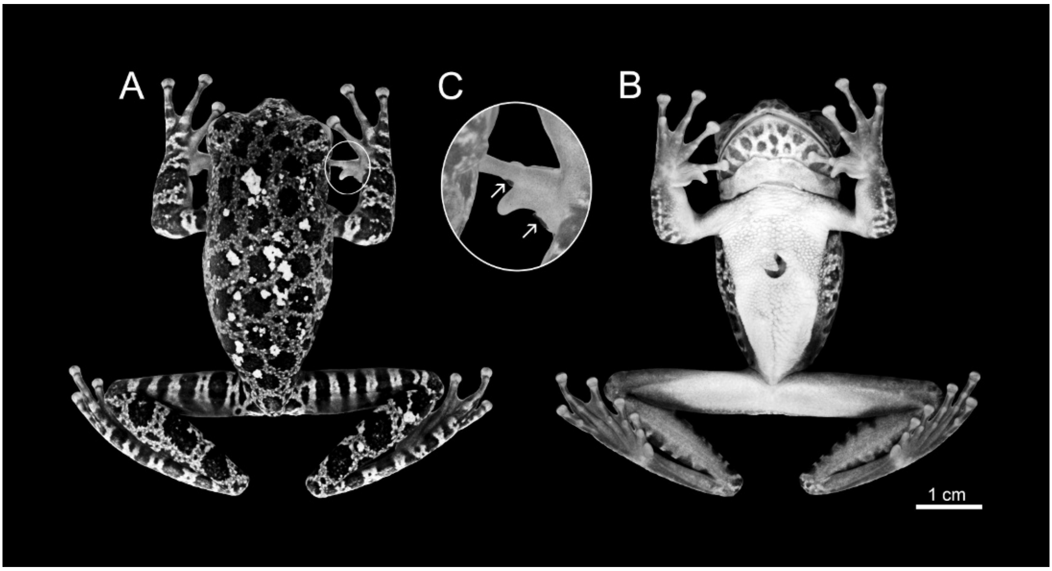

FIG. 1.—Dorsal (A), ventral (B), and close-up dorsal (C) view of the right hand of the holotype of *Bokermannohyla sagarana* sp. nov., UFMG 4246; arrows indicate the nuptial pad with two separate areas covered with small keratinized spiculae, on medial and lateral edge of the base of the prepollex. Adult male from Serra do Cabral, Municipality of Joaquim Felício, State of Minas Gerais, Brazil; SVL 47.4 mm.

and *B. saxicola* (TD/SVL 0.05; based on the average measures of 13 male specimens; Pombal and Caramaschi,1995).

The presence of macroscopically evident glandular tissue irregularly distributed on the mental area, extending backwards up to the beginning of the gular region distinguishes *B. sagarana* from *B. alvarengai* and *B. oxente*, in which these glands have been not found (Faivovich et al., 2009).

Males of *B. sagarana* have less hypertrophied forearms and less developed prepollex than *B. alvarengai*; more hypertrophied forearms and more developed prepollex than *B. itapopy*, *B. oxente*, and *B. saxicola*; and forearms and prepollex of similar proportions in relation with *B. ibitiguara* and *B. pseudopseudis* (Fig. 4).

The new species has nuptial pads with two separated areas covered with small keratinized spiculae on medial and lateral edge of the base of the prepollex (Fig. 1C), a character not found in the remaining species of the *B. pseudopseudis* group, although it is present in some species of the *B. circumdata* group (i.e., *B. lucianae*, *B. hylax*, *B. gouveai*, *B. circumdata*, *B. caramaschi*; A. C. Calijorne, personal communication).

In life, the dorsum color pattern that looks like lichens encrusted on rocks (Figs. 1A, 3) resembles *B. sagarana* to *B. itapoty* and *B. alvarengai*, although there are some differences in coloration. The dorsum of the new species is light gray (background) with dark gray blotches (without a central light spot) and white blotches scattered irregularly, whereas in *B. itapoty* the background is yellow to white–cream with black blotches of irregular shape that possess central light spots (Fig. 5C), and in *B. alvarengai* the dorsum varies from gray, with dark brown blotches similar to those of *B. itapoty* (with a central light spot) to uniformly gray (Fig. 5A). Although *B. ibitiguara*, *B. oxente*, *B. pseudopseudis*, and *B. saxicola* may have irregularly shaped blotches in their dorsum (giving them sometimes a lichenous aspect); they are usually less numerous and the background color tends to be brown or yellow and not to gray as in *B. sagarana* (Fig. 5).

Additionally, the new species differs from *B. itapoty*, *B. ibitiguara*, *B. saxicola*, *B. oxente*, and *B. pseudopseudis* by having dark gray perpendicular bars on the whole dorsal surface of thighs, rarely branched, without light spots, highly contrasted with the background color

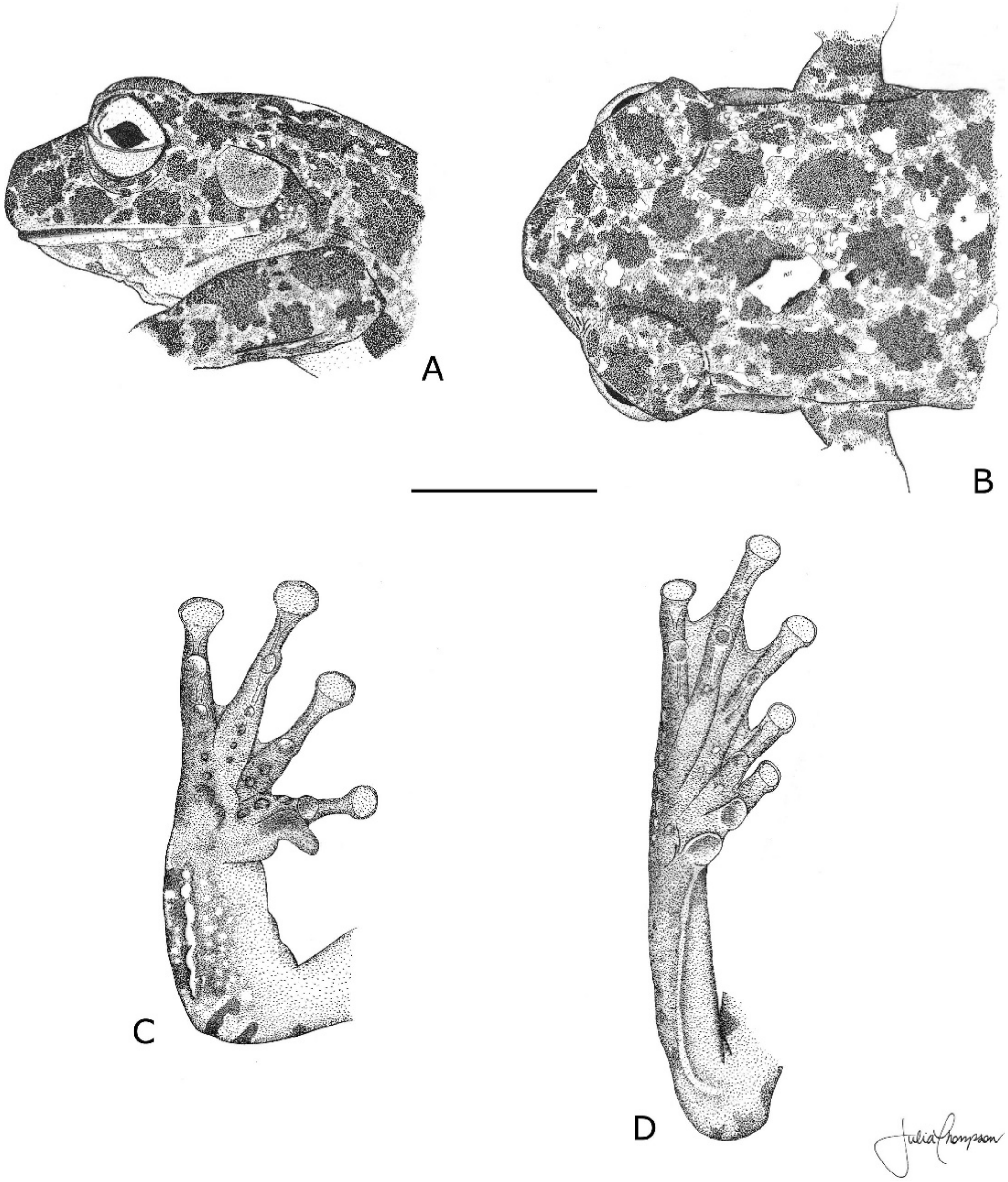

FIG. 2.—Holotype of *Bokermannohyla sagarana* sp. nov., UFMG 4246: (A) head in lateral view, (B) head in dorsal view, (C) left hand in ventral view, (D) left foot in ventral view. Horizontal line equals 10 mm.

(with light spots in *B. itapoty*; branched in *B. ibitiguara* and *B. saxicola*; occurring only in the median portion of dorsal surface and less evident in *B. oxente*, and less evident in *B. pseudopseudis*; Fig. 5). A white stripe over the vent distinguishes *B. saxicola* and *B. oxente* from *B. sagarana*, which lacks such stripe.

Description.—A species of the *B. pseudopseudis* group characterized by the following combination of traits: male SVL 48.9 ± 2.6 (range = 47.3–54.8 mm, *n* = 7), female SVL 46.6 ± 2.9 (range = 44.5–48.6 mm, *n* = 2), short snout, truncate in lateral and dorsal views; head 1.03 ± 0.02 times wider than long

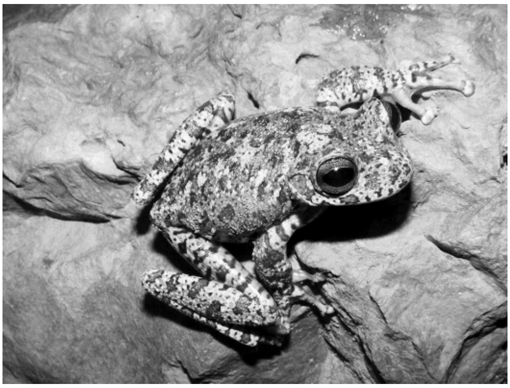

FIG. 3.—Living adult male of *Bokermannohyla sagarana* sp. nov. Paratopotype, UFMG 4238, SLV 47.9 mm, from Serra do Cabral, Municipality of Joaquim Felício, State of Minas Gerais, Brazil. Photo by: L. O. Drummond.

on average (range = 1.01–1.07, *n* = 9); tympanum diameter 0.08 ± 0.01 times SVL on average (range = 0.08–0.09; *n* = 9); hypertrophied forearm; well developed prepollex; nuptial pad small, with two separate areas covered with small keratinized spiculae, on medial and lateral edge of the base of the prepollex; dorsal color pattern composed of dark-gray blotches of irregular shape on a light gray background, without a central light spot, resembling lichens incrusted on rocks; dark-gray perpendicular bars covering the whole dorsal surface of thighs, rarely branched, without light spots, highly contrasted with the background color; and the lack of a white stripe over the vent.

Description of the holotype.—Adult male of moderate size for the *Bokermannohyla pseudopseudis* species group, SVL 47.4 mm (Fig. 1). Head 0.9 times wider than long, and as wide as trunk; head width 37.5% SVL; head length 36.6% SVL. Snout short and truncate in dorsal and lateral views (Fig. 2A,B). Canthus rostralis weakly evident. Loreal region slightly concave. Lips not flared. Nares slightly protuberant, directed laterally. Internarial region and top of head flat. Interorbital distance shorter than upper eyelid. Eye prominent, anterolaterally oriented, its diameter larger than eye–nostril distance. Tympanum evident, rounded, slightly deflected posteriorly toward the longitudinal body axis and dorsally, so the whole tympanum is nearly visible from above, its diameter 72% of eye diameter. Supratympanic fold distinct from posterior corner of eye to shoulder, covering dorsal margin of tympanic membrane.

Vomerine teeth in two contiguous slightly curved series, making an obtuse angle, posteriorly and between the choanae; each series bears 10 (right) and 8 (left) teeth. Choanae kidney shaped, separated by a distance slightly larger than two times maximum diameter. Tongue ovoid, attached overall (narrowly free around lateral and posterior margin). Vocal slits present, longitudinal, originating on the sides of the tongue and extending to the corner of the mouth. Vocal sac evident, single and subgular, slightly differentiated externally (Fig. 1B). Macroscopically evident glandular tissue irregularly distributed on the mental area, extending backwards up to the beginning of the gular region.

Forearms hypertrophied in relation to upper arms (Figs. 1, 2C, 4B). A row of small, low and almost continuous granules along

TABLE 1.—Measurements (in millimeters) of males and females of *Bokermannohyla sagarana* paratopotypes from Serra do Cabral, Espinhaço Range, State of Minas Gerais, Brazil.

	Males (*n* = 7)		Females (*n* = 2)
	Mean ± SD	Range	Range
Snout–vent length	48.9 ± 2.6	47.0–54.8	44.5–48.6
Head length	17.9 ± 0.5	17.4–18.8	16.0–16.3
Head width	18.3 ± 0.5	17.8–19.0	16.8–17.1
Eye diameter	5.6 ± 0.3	5.2–6.0	5.2–5.4
Tympanum diameter	4.1 ± 0.1	3.9–4.3	3.4–3.8
Interorbital distance	6.2 ± 0.4	5.6–7.0	5.6–5.9
Eye–nostril distance	4.8 ± 0.2	4.6–5.0	4.0–4.5
Internarial distance	3.9 ± 0.2	3.6–4.3	2.9–3.0
Thigh length	25.3 ± 0.9	24.3–26.8	24.8–25.2
Tibia length	25.7 ± 0.7	24.7–26.6	24.8–25.0
Foot length	19.1 ± 0.8	17.8–20.1	17.2–17.5

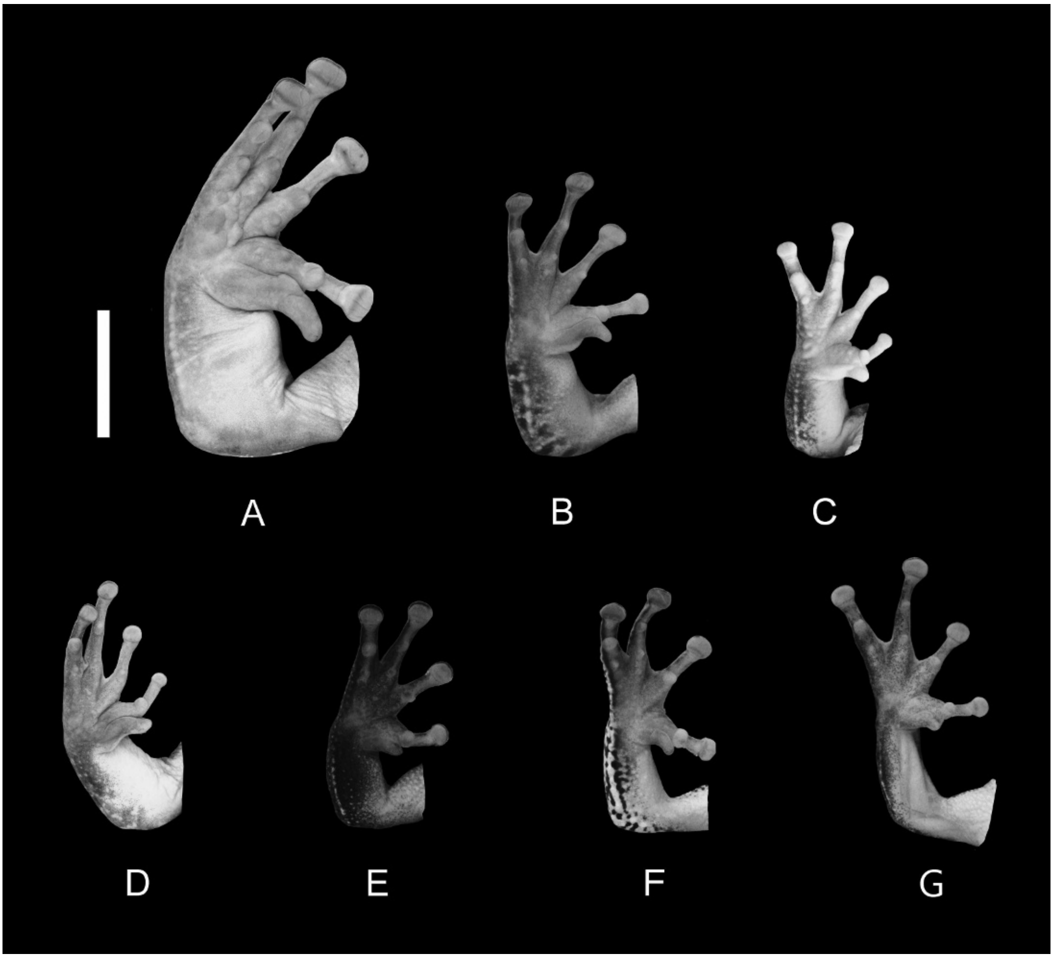

FIG. 4.—Development of forearm and prepollex of males of *Bokermannohyla pseudopseudis* species group. (A) *Bokermannohyla alvarengai* UFMG 5581, (B) *B. pseudopseudis* MNRJ 35096, (C) *Bokermannohyla sagarana* UFMG 4246 (holotype), (D) *Bokermannohyla ibitiguara* MZUFV 4588, (E) *Bokermannohyla oxente* UFMG 6255, (F) *Bokermannohyla itapoty* UFMG 4231, (G) *Bokermannohyla saxicola* UFMG 7678. Horizontal line equals 10 mm.

ventrolateral edge of forearm, from the base of hand to elbow. Fingers with elliptical discs; width of disc of Finger III equals to 54% tympanum diameter. Relative lengths of Fingers I < II < IV < III. Fingers webbed basally, with a slight dermal fringe; webbing formula of outer Fingers I–II 2^{+}–3^{+} III 3–$2^{1/2}$ IV. Subarticular tubercles rounded and well developed; distal tubercles on Fingers I, III, and IV ovoid, distal tubercle of Finger II conical. Supernumerary tubercles distinct, numerous. Outer metacarpal tubercle differentiated, nearly cordiform and bifid. Inner metacarpal tubercle large, its shape contouring the underlying distal prepollex that is modified into a well-developed, curved, protruding, and simple spine; fringe of skin joins the inner margin of the distal free section of the prepollex and the base of Finger I at the level of the subarticular tubercle. Nuptial pad small, with two discontinuous areas covered with small keratinized spiculae, on medial and lateral edge of the base of the prepollex.

Tibia length 54% SVL; foot length 38% SVL. Calcar absent; tarsal fold absent; subtle dermic ridge along the inner margin of the tarsus, starting in the tibiotarsal articulation and reaching the base of inner metatarsal tubercle; low granules discontinuously spaced

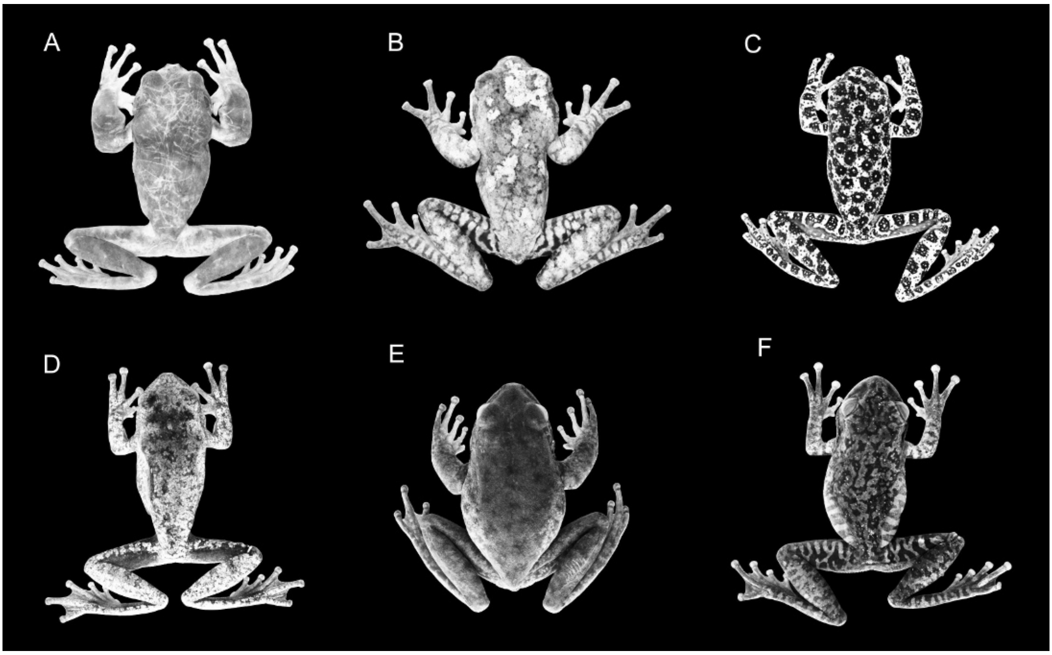

FIG. 5.—Dorsal view of the species of the *Bokermannohyla pseudopseudis* group. (A) *Bokermannohyla alvarengai* male UFMG 5143, SVL 76.0 mm; (B) *Bokermannohyla ibitiguara* male MZUFV 4588, SVL 35.9 mm; (C) *Bokermannohyla itapoty* male UFMG 4231, SVL 38.70 mm; (D) *Bokermannohyla oxente* male UFMG 7813, SVL 43.1 mm; (E) *Bokermannohyla pseudopseudis* male MNRJ 35096, SVL 44.1 mm; (F) *Bokermannohyla saxicola* male UFMG 6674, SVL 51.8 mm.

along outer edge of tarsus, from the first phalange of Toe V to heel. Inner metatarsal tubercle distinct, elliptical; outer metatarsal tubercle small, round. Toes bearing discs smaller than those on fingers; relative length I < II < III ≈ V < IV; webbing formula I 2^{-}–2^{+} II 1^{+}–2 III $1^{1/2}$–3^{-} IV 2^{+}–$1^{1/2}$ V. Subarticular tubercles distinct, round; supernumerary tubercles evident, numerous. Cloacal opening directed posteriorly at upper level of thighs; some flat, irregular, whitish tubercles scattered around and below cloaca. Texture of dorsal skin finely granular to granular in the dorsolateral region; throat, ventral surface of tibia, and posterior face of thigh smooth; chest, belly, and ventral surface of thighs granular. Ventral surface of arm slightly granular. Pectoral fold absent.

Measurements of the holotype (mm).—SVL 47.4; HL 17.4; HW 17.8; ED 5.9; TD 4.3; IOD 6.4; END 5.0; IND 3.7; THL 24.6; TBL 25.8; FL 18.7.

Color in life.—Dorsum background of the holotype color gray with irregularly shaped dark gray blotches, evenly distributed (Fig. 1). Few irregularly shaped light gray blotches irregularly distributed on head and dorsum. Upper surfaces of arms, legs, Fingers III and IV, and Toes IV and V with the same color pattern of dorsum. Granules along ventrolateral edge of forearm and outer edge of tarsus white. Dark-gray perpendicular bars covering the whole dorsal surface of thighs with thin dark gray stripes broken or not between bars, rarely branched, without light spots, highly contrasted with the background color. Fingers I and II and Toes I, II and III, posterior surface of thigh, and ventral surfaces of hand, foot, tarsus, and tibia grayish brown. Flanks gray with dark gray vertical blotches tending to form stripes. Venter and ventral surfaces of thighs and arms white–cream. Throat white–cream with gray blotches. Vocal sac cream. Tympanum gray. Iris golden yellow with black vermiculation.

Color in alcohol (70%).—In preservative, coloration is very similar to that of living adult, with colors becoming faded.

Variation.—Measurements of seven adult males and two adult females are presented in Table 1. Males are larger than females. Adult males with forearm more robust than adult females. The female prepollex is smaller and not sharp when compared to males. Throat of females with fewer spots than males. All individuals with light gray blotches on dorsum, but they vary in shape, size, number, and position. Two males (UFMG 4242, 4244) have the flanks with small rounded spots instead of vertical blotches. In one male (UFMG 4244) the thigh pattern is not composed of well-defined dark gray bars, but of small rounded spots instead. Gray blotches of the gular region can vary in number and intensity of color. The largest adult male (UFMG 4245) holds a more pigmented nuptial pad.

Etymology.—The specific name, a noun in apposition, honors the literary work of João Guiramães Rosa, a Brazilian novelist born in the 20th century. Sagarana was his first published book in which he exposed his innovative language and its themes associated to the Sertão (semiarid Brazilian backlands) life in the State of Minas Gerais, Brazil. Sagarana is a vocabulary made up by the author with the elements *saga* (common designation to prose narratives, historical or legendary, Nordic, written mainly in Iceland, in the 13th and 14th centuries), and *rana* (Tupi suffix that expresses similarity), meaning narratives similar to legends, sagas (Martins, 2001). Sagarana is cited by its author as an example of the expressive strength of a neologism, as it is totally new, for any reader and not explained yet, virgin of sight and understanding. We appropriated the innovative features of a neologism to name the new species.

Geographic distribution.—Bokermannohyla sagarana is known from the Municipalities of Joaquim Felício and Buenópolis, both from the Serra do Cabral, Espinhaço Range, State of Minas Gerais, southeastern Brazil. The species was recorded at the Parque Estadual da Serra do Cabral (Serra do Cabral State Park), Municipality of Buenópolis, State of Minas Gerais, Brazil, based on its advertisement call.

Natural History.—Bokermannohyla sagarana occurs in rocky mountain meadows called Campo Rupestre, a typical phytophysiognomy of the Espinhaço Range. For a characterization of the Campo Rupestre flora see Giulietti et al. (1987) and Harley (1995). For a characterization of the Espinhaço Range anurofauna see Leite et al. (2008). Adults were active at night, mainly close to small temporary rocky streams, but also on wet rock outcrops and in gallery forests of permanent streams. Males called on stones or in rock crevices and were founded in high densities during the beginning of rainy season (December). Calling activity began at sunset and continued throughout the night.

Conservation.—The Espinhaço Range is characterized by high species richness and a great degree of endemism of anuran species (Leite et al., 2008). It harbors five of seven known species of the *B. pseudopseudis* group and possibly is the most diverse area for this group. Although well sampled in some localities (e.g., Serra do Cipó; see Eterovick and Sazima, 2004; Leite et al., 2008, and references therein), most of its area, including the Serra do Cabral, remains virtually unexplored for amphibians (Leite et al., 2008). Despite the incipient sampling, the Serra do Cabral already harbors two recently described endemic amphibian species (*Scinax cabralensis*; Drummond et al., 2007; and *B. sagarana*). In the past few decades much of the natural landscapes of Serra do Cabral have been replaced by *Eucalyptus* and *Pinus* plantations. As silviculture is an economic activity that is increasingly common in the region, populations of the endemic anurans of Serra do Cabral will probably be affected by habitat loss and fragmentation. The only conservation unit of the region is the recently created (2005) and poorly structured Parque Estadual da Serra do Cabral. It has only 22,494 ha and protects a small portion of the local landscape.

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Appendix I

Specimens Examined

Bokermannohyla alvarengai: All from the State of Minas Gerais, Brazil. UFMG 666–667, 674 (males), Municipality of Catas Altas; UFMG 671 (male), 672 (female), Municipality of Santana do Riacho; UFMG 5143 (male), Municipality of Ouro Branco; LZV 632–633, 460–462 (males), Municipality of Ouro Branco; UFMG 5581 (male), Municipality of Rio Pardo de Minas; MNRJ 37275–76, 39026, 45359, Serra do Cipó, Municipality of Santana do Riacho.

Bokermannohyla ibitiguara: MZUFV 4586–4589 (males), Parque Nacional da Serra da Canastra, Municipality of São Roque de Minas, State of Minas Gerais, Brazil.

Bokermannohyla itapoty: UFMG 4601–02, 4604–05, 4231–36 (males), Municipality of Ibicoara, State of Bahia, Brazil.

Bokermannohyla oxente: All from the State of Bahia, Brazil. UFMG 5957 (male), Municipality of Rio de Contas; UFMG 6221–23, 6246, 6249, 6254–56, 6263, 6265 (males), Municipality of Campo Formoso; UFMG 7813 (male), Municipality of Rio de Contas.

Bokermannohyla pseudopseudis: All from the Goiás, Brazil. MNRJ 35096 (male), Municipality of Silvânia; MNRJ 3001 (male), 13024 (female), Municipality of Amaro Leite.

Bokermannohyla saxicola: all from the State of Minas Gerais, Brazil. UFMG 828, 830 (males), 818 (females), Municipality of Santana do Riacho; UFMG 840 (male), Municipality of Presidente Kubichek; UFMG 829 (male), Municipality of Serro; UFMG 3801 (female), Municipality of Botumirim; UFMG 7678 (male), Municipality of Joaquim Felício; UFMG 6674 (male), Municipality of Congonhas do Norte; MNRJ 3974, 14204 (paratypes), 17169–71, 17302, 38727, 39336–37, Serra do Cipó, Municipality of Santana do Riacho; MNRJ 17022, Municipality of Santa Luzia; MNRJ 17269–71, Municipality of Botumirin; MNRJ 17302–04, Municipality of Berilo.

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A NEW SPECIES OF THE *BOKERMANNOHYLA PSEUDOPSEUDIS* GROUP FROM THE ESPINHAÇO RANGE, CENTRAL BAHIA, BRAZIL (ANURA: HYLIDAE)

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Abstract: We describe a new species of the *Bokermannohyla pseudopseudis* group from Chapada Diamantina, Espinhaço Range, central Bahia, northeastern Brazil. It is characterized by the following combination of traits: male snout–vent length (SVL) 60.0 ± 3.3 (51.9–65.3 mm, $n = 14$); female SVL (60.2–61.6 mm, $n = 2$); short snout, rounded in dorsal view, rounded to truncate in lateral view; head 1.07 ± 0.04 (1.01–1.14 mm, $n = 14$) times wider than long; tympanum diameter 0.07 ± 0.01 (0.06–0.08 mm, $n = 14$) times SVL; macroscopically evident glandular tissue irregularly distributed on the mental area; hypertrophied forearm; well-developed prepollex; nuptial pad between the distal free section of the prepollex and the base of finger I; dorsum light gray to light brown (background) with irregular-shaped brown marbled blotches (without a central light spot) formed by small dark brown dots; in life, small yellow dots on upper and lower lips, eyelids, loreal and gular regions, supratympanic fold, fingers, arms, forearms, flanks, feet, tibiae, thighs, and cloacal region.

Key words: Amphibia; *Bokermannohyla flavopicta*; Campos Rupestres; Chapada Diamantina; Cophomantini; Endemism; Taxonomy

The genus *Bokermannohyla* occurs only in the Brazilian Atlantic Forest, Cerrado, and Caatinga biomes, and currently comprises 30 species (Leite et al., 2011). Based on a phylogenetic analysis and hypotheses by previous authors, Faivovich et al. (2005) recognized four species groups in this genus (*Bokermannohyla circumdata*, *B. claresignata*, *B. martinsi*, and *B. pseudopseudis*). Faivovich et al. (2005) recognized a *B. pseudopseudis* species group that includes *B. alvarengai*, *B. ibitiguara*, *B. pseudopseudis*, and *B. saxicola*. Lugli and Haddad (2006a) proposed the *B. alvarengai* species group for *B. alvarengai* and *B. itapoty*, based on their similar morphological and behavioral characteristics. Faivovich et al. (2009) argued that, as there are no known synapomorphies for the remaining species of the *B. pseudopseudis* group, the recognition of a *B. alvarengai* species group has the potential to make the *B. pseudopseudis* species group paraphyletic. Therefore, we prefer not to recognize the *B. alvarengai* species group.

The *Bokermannohyla pseudopseudis* species group currently includes *B. alvarengai*, *B. ibitiguara*, *B. pseudopseudis*, *B. saxicola*, *B. oxente*, *B. itapoty*, and *B. sagarana* (Leite et al., 2011). It is distributed in mountains of the Espinhaço Range in the states of Minas Gerais (*B. alvarengai*, *B. saxicola*, and *B. sagarana*) and Bahia (*B. itapoty* and *B. oxente*), Serra da Canastra in the state of Minas Gerais (*B. ibitiguara*), and Planalto Central (Central Plateau) in the state of Goiás and Federal District (Brasília; *B. pseudopseudis*), Brazil. During field expeditions to the summits of Chapada Diamantina, a regional designation of the Espinhaço Range in the state of Bahia, northeastern Brazil, we collected specimens of a new species of the *B. pseudopseudis* group, which we describe in this study.

Materials and Methods

Specimens used in the description or examined for comparisons are deposited in the following Brazilian institutions: UFMG (Universidade Federal de Minas Gerais, Belo Horizonte, Minas Gerais); MZUFV (Museu de História Natural João Moojen de Oliveira, Universidade Federal de Viçosa, Viçosa, Minas Gerais); LZV (Laboratório de Zoologia dos Vertebrados, Universidade Federal de Ouro Preto, Ouro Preto, Minas Gerais); and

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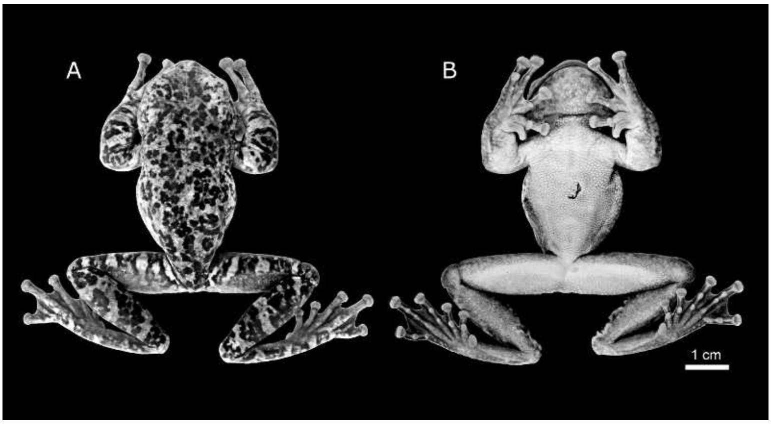

FIG. 1.—Dorsal (A) and ventral (B) views of the holotype of *Bokermannohyla flavopicta* sp. nov., UFMG 4989. Adult male from Serra das Almas, municipality of Rio de Contas, state of Bahia, Brazil. Snout–vent length 63.9 mm.

MNRJ (Museu Nacional, Rio de Janeiro, Rio de Janeiro). Webbing formula notation follows Savage and Heyer (1967), as modified by Myers and Duellman (1982). Measurements of adult specimens were taken with Mitutoyo digital calipers to the nearest 0.1 mm, and follow Duellman (1970), with the exception of thigh length. Abbreviations used in the measurements are SVL (snout–vent length), HL (head length), HW (head width), ED (eye diameter), TD (tympanum diameter), IOD (interorbital distance), END (eye–nostril distance), IND (internarial distance), THL (thigh length), TBL (tibia length), and FL (foot length, excluding tarsus, as in Duellman, 1970). Characters used for species comparisons were taken from Bokermann (1956), Sazima and Bokermann (1977), Lugli and Haddad (2006a) for *B. alvarengai*; Bokermann (1956), Pombal and Caramaschi (1995), Lugli and Haddad (2006b) for *B. saxicola*; Pombal and Caramaschi (1995), Lugli and Haddad (2006b) for *B. pseudopseudis*; Cardoso (1983), Lugli and Haddad (2006b) for *B. ibitiguara*; Lugli and Haddad (2006a) for *B. itapoty*; Lugli and Haddad (2006b) for *B. oxente*; Leite et al. (2011) for *B. sagarana*; and from specimens listed in the Appendix. Morphometric features from the literature were often not available as individual measurements, instead showing only average values, ranges, or not mentioning sample sizes (*n*). In these cases, measurements were presented as ranges (min–max), and ratios were calculated by dividing average values; therefore they are shown without ranges or sample sizes. We determined sex by the presence or absence of secondary sexual characters (forearm hypertrophy, prepollical spine, and vocal slits). The datum used for geographic coordinates was WGS84.

SPECIES DESCRIPTION

Bokermannohyla **flavopicta** *sp. nov.*

(Figs. 1–3, Table 1)

Holotype.—UFMG 4989, adult male, Serra das Almas, 13°31′13.9″S, 41°57′31.2″W, 1581 m above sea level, municipality of Rio de Contas, state of Bahia, Brazil, 13 January 2010, F.S.F. Leite; M.R. Lindemann, and R.B. Mourão (Figs. 1 and 2).

Paratypes.—UFMG 4984, adult male, 13°31′27.1″S, 41°57′27.9″W, 1559 m above sea level; UFMG 4985–4988, 4990, adult males, 13°31′13.9″S, 41°57′31.2″W, 1581 m above sea level; all collected at the type locality by F.S.F. Leite, M.R. Lindemann, and R.B. Mourão on 09 13 January 2010. UFMG 4506, adult male, 12 December 2009, 13°22′13.1″S, 41°52′40.8″W, 1616 m above sea level (Fig. 3); UFMG 4538, adult female, 15 December 2009, 13°22′30.1″S, 41°53′38.7″W, 1597 m above sea level; both collected at Serra do Itobira, municipality of Rio de Contas, state of Bahia, Brazil, by F.S.F. Leite; P.P.D. Pinheiro, and F. Fernandes. UFMG 7902–7903, 7905–7908, adult males, and UFMG 7904, adult

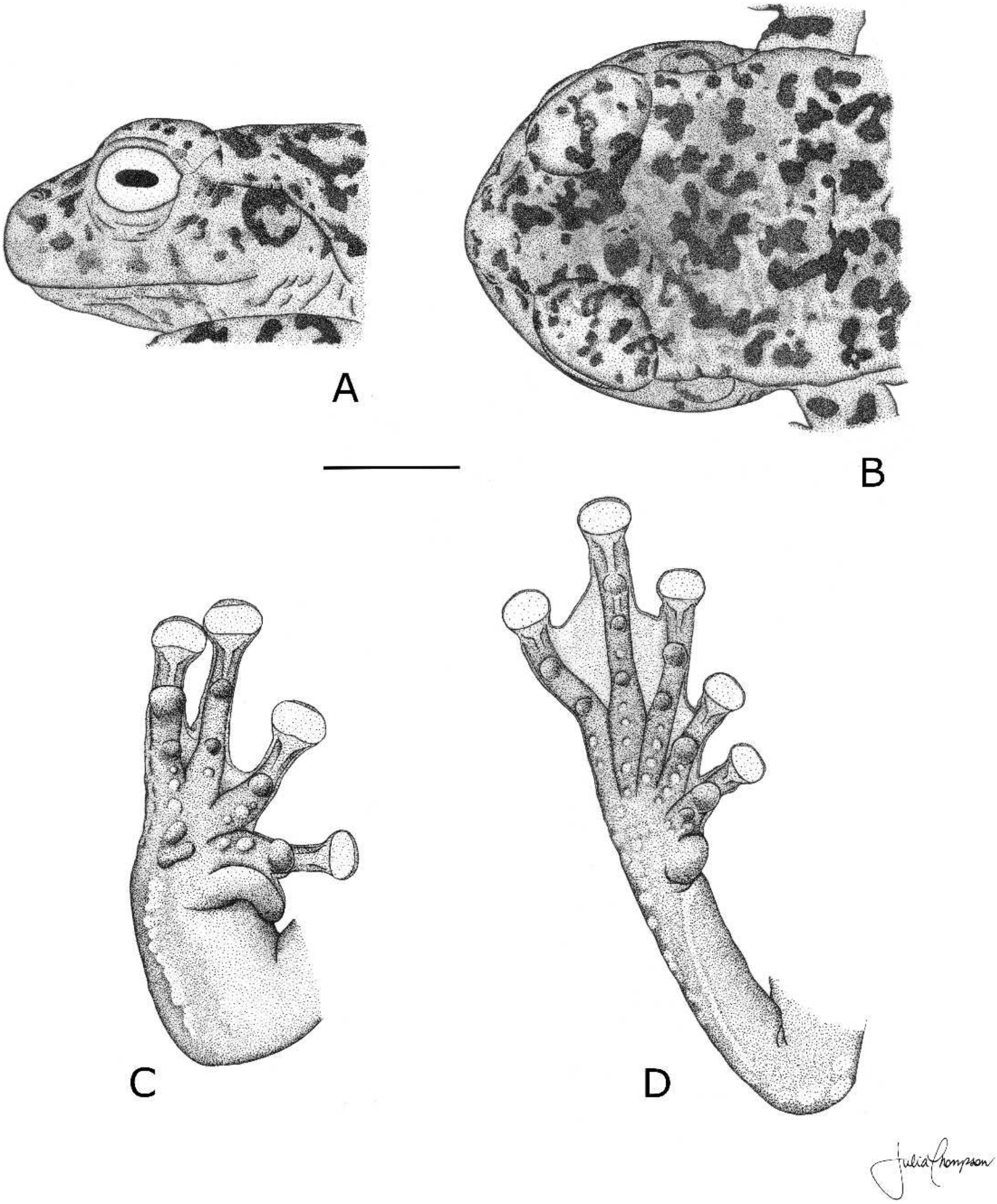

Fig. 2.—Holotype of *Bokermannohyla flavopicta* sp. nov., UFMG 4989: (A) Head in lateral view; (B) head in dorsal view; (C) right hand in ventral view; (D) right foot in ventral view. Horizontal line equals 10 mm.

female, 16 January 2010, Serra do Bastião, 13°04′39.5″S, 41°38′36.2″W, 1473 m above sea level, municipality of Mucugê, state of Bahia, Brazil, by T.L. Pezzuti; L.O. Drummond, B. Imai, and L. Rodrigues.

Diagnosis.—The dorsal color pattern composed of small dark brown blotches in a light gray to light brown (background), resembling lichens encrusted on rocks, distinguishes *B. flavopicta* (Figs. 1 and 3) from all species of

FIG.. 3.—Living adult male of *Bokermannohyla flavopicta* sp. nov. Paratype, UFMG 4506, snout–vent length 59.7 mm, from Serra das Almas, municipality of Rio de Contas, state of Bahia, Brazil. Photograph by F.S.F. Leite.

the *B. circumdata* group, which have a brown dorsum (without or with few blotches), and from all species of the *B. claresignata* group, which have a yellow to beige dorsum. The absence of a ventral humeral crest developed as a spine in males distinguishes *B. flavopicta* from all species of the *B. martinsi* species group.

Males of *B. flavopicta* (SVL 51.9–65.3 mm, *n* = 14) are larger than males of *B. itapoty* (SVL 37.8–46.3 mm, *n* = 12), *B. oxente* (SVL 38.8–43.4 mm, *n* = 14), and *B. ibitiguara* (SVL 31.1–44.1 mm, *n* = 8); are generally larger than males of *B. sagarana* (SVL 47.3–54.8 mm, *n* = 7) and *B. saxicola* (SVL 39.6–55.0 mm, *n* = 8), although there is some overlap; and are smaller than males of *B. alvarengai* (SVL 86.0–105.0 mm, *n* = 9). Females of *B. flavopicta* (SVL 60.2–61.6 mm, *n* = 2) are larger than females of *B. pseudopseudis* (SVL 41.0–43.0 mm; *n* = 2), *B. ibitiguara* (SVL 43.4–43.5 mm, *n* = 2), *B. oxente* (SVL 39.5–44.5 mm, *n* = 5), *B. sagarana* (SVL 44.5–48.6 mm, *n* = 2), *B. itapoty* (SVL 43.4–50.2 mm, *n* = 3), and *B. saxicola* (SVL 40.0–50.9 mm, *n* = 5), and smaller than females of *B. alvarengai* (SVL 68.0–82.0 mm, *n* = 5).

Bokermannohyla flavopicta have heads 1.01–1.14 times wider than long (*n* = 14; Table 1), as do the remaining species of the *B. pseudopseudis* group, with the exception of *B. oxente,* in which the heads are as long as wide (1.0 times wider than long; based on the average measures of 14 male specimens; Lugli and Haddad, 2006b), and *B. saxicola*, in which the heads are 1.14 times longer than wide (based on average measures of 13 male specimens; Pombal and Caramaschi, 1995).

The new species appears to have a slightly larger tympanum (TD/SVL 0.06–0.08; *n* = 14) than *B. saxicola* (TD/SVL 0.05, based on an average of 13 male specimens; Pombal and Caramaschi, 1995), although the values are very similar.

TABLE 1.—Measurements (in millimeters) of *Bokermannohyla flavopicta* sp. nov., type series from Serra das Almas, Serra do Itobira, and Serra do Bastião, state of Bahia, Brazil.

	Males (*n* = 14)		Females (*n* = 2)
	Mean ± SD	Range	Range
Snout–vent length	60.0 ± 3.3	51.9–65.3	60.2–61.6
Head length	20.8 ± 0.9	19.4–23.1	20.7–21.6
Head width	22.0 ± 0.7	21.1–23.2	21.5–23.9
Eye diameter	6.1 ± 0.6	4.3–6.7	6.0–6.5
Tympanum diameter	4.1 ± 0.4	3.4–4.9	4.0–4.4
Interorbital distance	7.9 ± 0.5	7.0–8.5	7.7–8.3
Eye–nostril distance	5.1 ± 0.5	4.3–5.8	4.6–4.9
Internarial distance	5.1 ± 0.4	4.5–5.7	5.1–5.8
Thigh length	33.7 ± 1.5	31.5–35.8	34.7–35.7
Tibia length	34.5 ± 2.0	30.5–36.9	36.1–36.6
Foot length	26.1 ± 1.1	24.3–28.0	25.7–27.0

The presence of macroscopically evident glandular tissue irregularly distributed on the mental area, extending posteriorly to the beginning of the gular region, distinguishes *B. flavopicta* from *B. alvarengai* and *B. oxente*, in which these glands have not been found (Faivovich et al., 2009).

Males of *B. flavopicta* have less-hypertrophied forearms and a less-developed prepollex than *B. alvarengai*; more-hypertrophied forearms and a more-developed prepollex than *B. itapopy*, *B. oxente*, and *B. saxicola*; and forearms and prepollex of similar proportions to those of *B. ibitiguara*, *B. pseudopseudis*, and *B. sagarana* (Figs. 1 and 2C; see Fig. 4 of Leite et al., 2011, for comparison).

The presence of a nuptial pad between the distal free section of the prepollex and the base of finger I distinguishes the new species from *B. saxicola*, *B. pseudopseudis,* and *B. ibitiguara*, which lack this structure, and from *B. sagarana,* in which the nuptial pad has two discontinuous areas covered with small keratinized spiculae on the medial and lateral edges of the base of the prepollex.

In life, the presence of small yellow dots on upper and lower lips, eyelids, loreal and gular regions, supratympanic fold, fingers, arms, forearms, flanks, feet, tibiae, thighs, and cloacal region distinguishes *B. flavopicta* from all species of the *B. pseudopseudis* group, in which yellow dots are absent. The dorsal color pattern that looks like lichens encrusted on rocks (Figs. 1A and 3) is similar in *B. flavopicta*, *B. sagarana*, *B. itapoty*, and *B. alvarengai*, although there are some differences among these species. The dorsum of the new species is light gray to light brown (background) with irregularly shaped brown marbled blotches (without a central light spot) formed by small dark brown dots, whereas the dorsum in *B. sagarana* is light gray (background) with dark gray blotches (without a central light spot) and white blotches scattered irregularly, the background color in *B. itapoty* is yellow to white-cream with black blotches of irregular shape that possess central light spots, and the dorsum in *B. alvarengai* varies from gray with dark brown blotches similar to those of *B. itapoty* (with a central light spot) to uniformly gray (see Fig. 5 of Leite et al., 2011, for comparison). Although *B. ibitiguara*, *B. oxente*, *B. pseudopseudis*, and *B. saxicola* may have irregularly shaped blotches on their dorsum (giving them sometimes a lichenous appearance), they are usually less numerous than in *B. flavopicta* (see Fig. 5 of Leite et al., 2011).

Description.—A species of the *B. pseudopseudis* group characterized by the following combination of traits: male SVL 60.0 ± 3.3 (51.9–65.3 mm, *n* = 14); female SVL (60.2–61.6 mm, *n* = 2); short snout, rounded in dorsal view, rounded to truncate in lateral view; head 1.07 ± 0.04 (1.01–1.14, *n* = 14) times wider than long; tympanum diameter 0.07 ± 0.01 (0.06–0.08; *n* = 14) times SVL; macroscopically evident glandular tissue irregularly distributed on the mental area; hypertrophied forearm; well-developed prepollex; nuptial pad between the distal free section of the prepollex and the base of finger I; dorsum light gray to light brown (background) with irregularly shaped brown marbled blotches (without a central light spot) formed by small dark brown dots; in life, small yellow dots on upper and lower lips, eyelids, loreal and gular regions, supratympanic fold, fingers, arms, forearms, flanks, feet, tibiae, thighs, and cloacal region.

Description of the holotype.—Adult male, SVL 63.9 mm (Fig. 1). Head 1.02 times wider than long; head width 37.0% of SVL; head length 36.0% of SVL. Snout short, rounded in dorsal view, rounded to truncate in lateral view (Fig. 2A,B). Canthus rostralis weakly evident. Loreal region slightly concave. Nares slightly protuberant, directed laterally. Internarial region and top of head flat. Interorbital distance 1.65 times longer than upper eyelid. Eye prominent, anterolaterally oriented, its diameter 1.13 times larger than END. Tympanum evident, rounded, slightly deflected posteriorly toward the longitudinal body axis and dorsally such that almost the complete tympanum is visible from above, its diameter 74% of ED. Supratympanic fold distinct from posterior corner of eye to shoulder, covering dorsal margin of tympanic membrane.

Vomerine teeth in two contiguous slightly curved series, making an obtuse angle posteriorly and between the choanae, with each series bearing 9 (right) and 10 (left) teeth. Choanae kidney-shaped, separated by a distance larger than three times the maximum diameter. Tongue ovoid, attached overall (narrowly free around lateral and posterior margin). Vocal slits present, longitudinal, originating on the sides of the tongue and extending to the corner of the mouth. Vocal sac single, subgular, slightly differentiated externally (Fig. 1B). Macroscopically evident glandular tissue irregularly distributed on the mental area, extending backwards up to the beginning of the gular region.

Forearms hypertrophied in relation to upper arms (Figs. 1 and 2C). A row of small, low, and almost continuous granules along ventrolateral edge of forearm, from the base of hand to elbow (Figs. 1B and 2C). Fingers with elliptical discs; width of disc of finger III equals to 86% of tympanum diameter. Relative lengths of fingers I < II < IV < III. Fingers webbed basally, with a slight dermal fringe; webbing formula of outer fingers I–II2–3^+III$2^{2/3}$–2^+VI. Subarticular tubercles conical, well developed; distal tubercles on fingers II and V rounded, flat.

Supernumerary tubercles distinct, numerous. Outer metacarpal tubercle differentiated, divided. Inner metacarpal tubercle large, its shape contouring the underlying distal prepollex that is modified into a well-developed, curved, protruding, simple spine; fringe of skin joins the inner margin of the distal free section of the prepollex and the base of finger I at the level of the subarticular tubercle. Nuptial pad present, dorsal, covered with keratinized spiculae, between the distal free section of the prepollex and the base of finger I.

Tibia length 56% of SVL; foot length 42% of SVL. Calcar and tarsal fold absent; subtle dermic ridge along the inner margin of the tarsus, starting in the tibio-tarsal articulation and reaching the base of inner metatarsal tubercle; low granules discontinuously spaced along outer edge of tarsus, from the first phalange of toe V to heel. Inner metatarsal tubercle distinct, elliptical; outer metatarsal tubercle absent. Toes bearing discs smaller than those on fingers; relative length I < II < III ≈ V < IV; webbing formula I2^-–2^-II1–2III1–2IV$1^{1/2}$–1V. Subarticular tubercles distinct, round; supernumerary tubercles evident, numerous. Cloacal opening directed posteriorly at upper level of thighs; some flat, irregular, whitish tubercles scattered around and below cloaca. Dorsal and ventral skin sparsely granular to granular. Pectoral fold absent.

Measurements of the holotype (millimeters).—Snout–vent length 63.9; HL 23.0; HW 23.4; ED 6.6; TD 4.9; END 5.8; IND 5.2; IOD 8.2; THL 35.8; TBL 35.9; FL 26.7.

Color in life.—The dorsum of the new species is light gray to light brown (background) with irregularly shaped brown marbled blotches (without a central light spot) formed by small dark brown dots. Small yellow dots on upper and lower lips, eyelids, loreal and gular regions, supratympanic fold, fingers, arms, forearms, flanks, feet, tibiae, thighs, and cloacal region. Tympanum, dorsal surfaces of forearms, arms, tibia, feet, finger IV and base of finger III, and toes V and IV with the same color pattern of dorsum, tending to form stripes on forearms and tibiae. Dark gray perpendicular bars, with light gray blotches, covering the dorsal surface of thighs, with little contrast with the background color. Gray fingers I and II, toes I, II, and III, posterior surface of thighs, and ventral surfaces of hand, foot, tarsus, and tibia. Flanks with color pattern similar to that of dorsum, with background color in lighter tones. White tubercles scattered around and below cloaca, tending to form a stripe over the vent. Venter and ventral surfaces of arms and thighs white-cream. Throat and vocal sac grayish white with few gray dots of diffuse margins. Iris silver with black vermiculation; silver ring around pupil.

Color in 70% alcohol.—In preservative, coloration is very similar to that of living adult, but with faded colors. Small yellow dots lose their color and become indistinguishable.

Variation.—Measurements of 14 adult males and two adult females are presented in Table 1. Adult males with forearm more robust than in adult females. The female prepollex is smaller and not sharp compared to that of males. Dorsal marbled blotches formed by small dark brown dots vary in disposal shape, size, and position, giving some individuals a leopard-like color pattern. White stripe over the vent not present in many specimens. In life, small yellow dots vary in density, size, position, and color intensity. Gray dots in gular region can vary in number, contrast, and intensity of color. Webbing formula of outer fingers I–II(2, 2^{-})–(3^{+}, 3, 3^{-})III$2^{2/3}$–2^{+}VI and toes I(2^{-}, $1^{2/3}$)–2^{-}II1-2III(1, 1^{-})–2IV(2–$1^{1/2}$)–1V.

Etymology.—The specific epithet *flavopicta* derives from the combination of the Latin words *flavus* (yellow) and *pictus* (painted, colored), and refers to the small yellow dots of the new species in life.

Geographic distribution.—*Bokermannohyla flavopicta* is known from Serra das Almas, Serra do Itobira (municipality of Rio de Contas), and Serra do Bastião (municipality of Mucugê), southwestern Chapada Diamantina, Espinhaço Range, state of Bahia, northeastern Brazil. During extensive field trips conducted during two consecutive rainy seasons, we did not record *B. flavopicta* at the Parque Nacional da Chapada Diamantina (Chapada Diamantina National Park), on the eastern Chapada Diamantina, suggesting that its distribution is restricted to the highlands of southwestern Chapada Diamantina.

Natural History.—*Bokermannohyla flavopicta* occurs in high-elevation (above 1500 m above sea level) rocky mountain meadows called *Campos Rupestres*, a typical phytophysiognomy of the Espinhaço Range. For a characterization of the Campos Rupestres flora, see Giulietti et al. (1987) and Harley (1995). For a characterization of the Espinhaço Range anuran fauna, see Heyer (1999) and Leite et al. (2008). Males called on steep rock outcrops or in rock crevices, mainly close to small streams without gallery forests, which required us to climb to collect the specimens. The advertisement call could be heard from a long distance. We found the frogs in low densities during the beginning of rainy season (December–January).

Conservation.—The Espinhaço Range is characterized by high species richness of endemic anurans. Since the compilation of Espinhaço Range anuran endemics by Leite et al. (2008), seven new species have been described: *Hypsiboas botumirim* (Caramaschi et al., 2009), *Bokermannohyla juiju* (Faivovich et al., 2009), *Scinax tripui* (Lourenço et al., 2009), *Pleurodema alium* (Maciel and Nunes, 2010), *Physalaemus orophilus* (Cassini et al., 2010), *Proceratophrys minuta* (Napoli et al., 2011), and *B. flavopicta*. Baêta et al. (2009) demonstrated that *Phyllomedusa itacolomi* is a junior synonym of *P. ayeaye,* and therefore it is neither a valid species nor an Espinhaço endemic. Taucce et al. (2012) showed that *Ischnocnema izecksohni* should no longer be considered an Espinhaço endemic because it also occurs in other Brazilian mountain ranges. Therefore, 33 anuran species should currently be considered endemic to the Espinhaço Range (Leite et al., 2008; this study).

The description of the new species corroborates the hypothesis suggested by Leite et al. (2011) that the Espinhaço Range is the richest area in species of the *B. pseudopsedis* group. It harbors six (all endemic) of eight known species of this group. Despite its importance for conservation, northern Espinhaço Range in the state of Bahia (Chapada Diamantina) remains virtually unexplored for amphibians. If compared to the current 26 anuran endemic species of the southern Espinhaço (mostly located in the state of Minas Gerais and bordering Bahia), Chapada Diamantina (entirely located in the state of Bahia) contains few endemic species (only eight). Part of this disparity in endemic species richness is due to incipient sampling and taxonomic research on the anuran fauna of Chapada Diamantina in relation to southern Espinhaço. Many northern Espinhaço endemic species need to be described (F. Leite, personal observation).

Bokermannohyla flavopicta was registered at Área de Relevante Interesse Ecológico Pico das Almas and Área de Proteção Ambiental Serra do Barbado (Serra do Itobira), both of which are state protected areas of sustainable use (equivalent to IUCN categories IV and V, respectively; IUCN, 2004), and Parque Municipal Natural Serra das Almas, a small protected area of the municipality of Rio de Contas. However, despite being protected areas, these sites currently have limited conservation activities, management, and supervision. Therefore, disorderly land use and occupation, fire (from criminals and from agriculture or native pasture management for cattle breeding), and unregulated tourism are constant threats to *B. flavopicta* habitat. The species is not known to occur in strictly protected reserves (e.g., national parks, biological reserves, etc.; equivalent to IUCN categories I and II; IUCN, 1994).

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APPENDIX

Specimens Examined

***Bokermannohyla alvarengai*:** Brazil: state of Minas Gerais: UFMG 666–667, 674 (males), municipality of Catas Altas; UFMG 671 (male), 672 (female), municipality of Santana do Riacho; UFMG 3823 (female), municipality of Botumirim; UFMG 4018 (female), municipality of Congonhas do Norte; UFMG 5143 (male), municipality of Ouro Branco; UFMG 5385 (female), municipality of Morro do Pilar; LZV 632–633, 460–462 (males), municipality of Ouro Branco; UFMG 5581(male), municipality of Rio Pardo de Minas; MNRJ 37275–37276, 39026, 45359 (males), Serra do Cipó, municipality of Santana do Riacho. ***Bokermannohyla ibitiguara*:** Brazil: state of Minas Gerais: MZUFV 4586–4589 (males), Parque Nacional da Serra da Canastra, municipality of São Roque de Minas. ***Bokermannohyla itapoty*:** Brazil: state of Bahia: UFMG 4601–4602, 4604–4605, 4231–4236 (males), municipality of Ibicoara. ***Bokermannohyla oxente*:** Brazil: state of Bahia: UFMG 5957, 7813 (males), municipality of Rio de Contas; UFMG 6221–23, 6246, 6249, 6254-56, 6263, 6265 (males), municipality of Campo Formoso. ***Bokermannohyla pseudopseudis*:** Brazil: state of Goiás: MNRJ 35096 (male), municipality of Silvânia; MNRJ 3001 (male), 13024 (female), municipality of Amaro Leite. ***Bokermannohyla sagarana*:** Brazil: state of Minas Gerais: UFMG 4246 (holotype), 4238, 4240–4241 (paratypes), municipality of Joaquim Felício; UFMG 8614–8619, UFMG 8620–8621 (paratypes), municipality of Buenópolis. ***Bokermannohyla saxicola*:** Brazil: state of Minas Gerais: UFMG 828, 830 (males), 818 (females), municipality of Santana do Riacho; UFMG 840 (male), municipality of Presidente Kubitschek; UFMG 829 (male), municipality of Serro; UFMG 3801 (female), municipality of Botumirim; UFMG 7678 (male), municipality of Joaquim Felício; UFMG 6674 (male), municipality of Congonhas do Norte; MNRJ 3974, 14204 (paratypes), 17169–17171, 17302, 38727, 39336–39337, Serra do Cipó, municipality of Santana do Riacho; MNRJ 17022, municipality of Santa Luzia; MNRJ 17269–17271, municipality of Botumirim; MNRJ 17302–17304, municipality of Berilo.