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RESEARCH

Evaluating forest refugial models using species distribution models, model filling and inclusion: a case study with 14 Brazilian species

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ABSTRACT

Aim We aimed to assess the generality of existing models of late Quaternary biodiversity refugia in the Brazilian Atlantic forest by testing whether taxonomic identity and range descriptors influence the extent by which previously proposed models of forest (habitat) refugia successfully predict species' inferred refugial areas.

Location Brazilian rain forest.

Methods We compiled and filtered records of 14 animal species that belong to distantly related groups (spiders, harvestmen, scorpions, amphibians, birds, lizards and mammals) and show distinct distribution patterns within the Atlantic rain forest. Using MAXENT, we generated three distribution models for each species under different climatic scenarios (current, 6000 and 21,000 years ago). Species-specific historically stable areas (refugia) were identified through the intersection of the three models. We then measured the amount of 'inclusion' of species-specific refugia within published forest refugia, and quantified 'filling' of the biome refugia by species-specific refugia. The influence of taxonomic distance between species and range descriptors were analysed.

Results Current distribution models generated for the 14 species had high accuracy (AUC > 0.9). Inclusion and filling, two uncorrelated metrics, varied among species and were not influenced by taxonomic identity. Species range characteristics influenced forest model filling only, with higher values found in widely distributed species (i.e. occurring from Northeastern to Southeastern Brazil).

Main conclusions Species-specific and forest refugial areas are not necessarily the same. The power of forest refugial models to predict species-specific refugial area differs among species and may be influenced by range attributes. Species data suggests the existence of a large refugium in Southeast of Brazil, a result at odds with the currently available forest-wide models. The predictive power of forest refugial models is narrowed; we now better understand their applicability limits.

Keywords

Atlantic rain forest, conservation biogeography, MAXENT, paleoclimate modelling, Pleistocene and refugium.

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INTRODUCTION

Global climate underwent several cycles of glacial and interglacial periods throughout the Cenozoic (Barnosky, 2005), and the biological implications of such oscillations – particularly those in the Pleistocene – have been the focus of studies world-wide (Avise & Walker, 1998; Klicka & Zink, 1999; Stuart *et al.*, 2004; Bennett & Provan, 2008; Ceballos *et al.*, 2010). In temperate regions, abundant evidence supports the view that forested biomes contracted towards the equator during glacial periods (e.g. Petit *et al.*, 2002; Walker *et al.*, 2009; Aldenhoven *et al.*, 2010). The term refugium has been then applied to denote a forest fragment large enough to support a natural population during a glacial–interglacial cycle (Stewart *et al.*, 2009; Ashcroft, 2010). In the Neotropics, however, the existence, location and role of supposed glacial forest refugia have been a matter of debate (Prance, 1982; Colinvaux *et al.*, 1996; Haffer & Prance, 2001; Knapp & Mallet, 2003; Bush *et al.*, 2007). While a tropical refugial hypothesis was first proposed to explain biodiversity patterns in the Amazon forest (Haffer, 1969), its validity and its evolutionary implications are still debated (Haffer, 1992, 2008; Colinvaux *et al.*, 2000; Haffer & Prance, 2001; Bush & Oliveira, 2006; Rull, 2006; Bush *et al.*, 2007).

Recent studies in another forested system – the Brazilian coastal forests – have fuelled the debate about the putative role of late Quaternary forest refugia in the New World (Carnaval & Moritz, 2008; Carnaval *et al.*, 2009; Thomé *et al.*, 2010). This megadiverse yet threatened biome ranks among the top five priority areas for conservation worldwide and is known for its more than 8000 species of animals and plants, many endangered and endemic (Myers *et al.*, 2000). The Atlantic forest once stretched continuously along Brazil's coast, covering around 150 million ha, yet only about 11.7% of the original vegetation remains in the form of small fragments of second-growth forests in early to medium stages of succession (97% of them < 250 ha; Tabarelli *et al.*, 2005; Ribeiro *et al.*, 2009).

Using tools of climate-based correlative modelling, Carnaval & Moritz (2008) generated hypotheses about the spatial distribution of the Atlantic rain forest at 6000 and 21,000 years ago. By intersecting such hincasted models of forest distribution with a model of the current forest range, they identified regions of the Atlantic rain forest, which remained largely forested during the late Quaternary – which are here called as refugia. A striking conclusion afforded by that modelling exercise was that of large-scale differences between the spatial extent of late Quaternary forest refugia in the northern versus the southern forests of Brazil.

While Carnaval & Moritz's (2008) forest refugial model was corroborated by existing palaeo-palynological data sets (e.g. Behling, 1998; Ledru *et al.*, 2005), phylogeographic and population genetic studies set to evaluate the historical demographic implications of their hypothesis provided mixed support for the proposed location of forest refugial areas (Cabanne *et al.*, 2008; Carnaval & Moritz, 2008; Carnaval *et al.*, 2009; Fitzpatrick *et al.*, 2009; Martins *et al.*, 2009; Mata *et al.*, 2009; Palma-Silva *et al.*, 2009; Ramos *et al.*, 2009; Brito & Arias, 2010; Novaes *et al.*, 2010; Thomé *et al.*, 2010; Ribeiro *et al.*, 2011). Whereas molecular data showed that the forest model correctly hypothesized the location of the Pleistocene refugia for lowland and mid-altitude species of *Hypsiboas* treefrogs, as well as other skinks, birds and bats (Cabanne *et al.*, 2008; Carnaval *et al.*, 2009; Martins *et al.*, 2009), they also demonstrated that the model fails to explain genetic patterns in frogs of the *Rhinella crucifer* group (Thomé *et al.*, 2010), and in the montane *Proceratophrys boiei* litter frog (Amaro *et al.*, 2012). In the present study, we explore possible reasons for this observed discord between species-specific molecular diversity data and the demographic predictions that emerge from the existing forest models.

Interspecific differences in the predictive power of general distribution models are often related to taxon-specific issues such as range size, habitat use, dispersal ability and geographic region of occurrence (Brown & Lomolino, 2006; Graham *et al.*, 2006; Hernandez *et al.*, 2006; McPherson & Jetz, 2007; Papes & Gauber, 2007). Yet, the relationship between these characteristics and the predictive power of forest refugial models is still underexplored. Here, we evaluate whether this can be a plausible reason for the mixed support given by species-specific genetic data sets to the existing Atlantic forest refugial model. To that end, we compile records and develop distribution models for 14 Atlantic rain forest animal species belonging to distantly related groups (spiders, harvestmen, scorpions, amphibians, birds, lizards and mammals). We use these data to test whether taxonomic identity and species-specific geographic distribution region, size of the distribution area and specialization in the use of physiognomies (forest formations with distinct species composition and structure) in the Atlantic forest influence how well species-specific refugial models match the available forest refugial model. This enables us to gauge at the influence of range-related species traits on the overall predictive power of forest refugial models in identifying species refugial areas. While our study focuses on the Atlantic rain forest, the approach and overall conclusions may be useful in other biological systems where habitat refugial models are tentatively applied to explain diversity patterns in a large number of species.

METHODS

Because the forest refugial model (Carnaval & Moritz, 2008) aimed to promote insight about diversity patterns of organisms restricted to forested areas, we limited our study to endemic animals of the Atlantic rain forest. We selected groups that were taxonomically resolved and well represented in scientific collections or in recent published revisions. We also aimed to broadly represent the terrestrial fauna that inhabit the biome, using two species from each of the following groups: spiders, harvestmen, scorpions, amphibians, birds, lizards and mammals.

We selected 14 species to represent: (1) different regional patterns of occurrence in the Atlantic rain forest, (2) distinct range sizes (distribution amplitude), and (3) different abilities to occupy the several phytophysiognomies of the Atlantic forest biome (Table 1), hence enabling a more powerful statistical evaluation of the factors influencing the predictive power of the forest refugial model.

We obtained occurrence records from 16 scientific collections and 145 scientific articles and books (see Appendix 1 in Supporting Information) and verified the accuracy of the geo-referenced data with DIVA-GIS v 7.3.0 (Hijmans *et al.*, 2002). To avoid data clustering (Nelson *et al.*, 1990; Hernandez *et al.*, 2006), we limited our database to a single record per km^2 per species. Wherever high spatial concentrations of records were evident, despite the subsampling procedure, we randomly removed records from the densely sampled region to obtain a more homogeneous distribution and to avoid bias (Phillips *et al.*, 2009; Elith *et al.*, 2010). After processing, the number of records per species ranged from 70 to 162. To standardize the influence of the sampling in model predictive power (Stockwell & Peterson, 2002; Papes & Gauber, 2007), we randomly selected 50 records for each species (see Table S1) to make the inter-specific results comparable. This number of records is adequate to generate accurate models of the species distribution at the spatial scale of this study (Hernandez *et al.*, 2006).

Generation of the species-specific refugial models

We used MAXENT (Phillips *et al.*, 2006; v 3.3.3e) to model species distributions, given its demonstrated effectiveness (Elith *et al.*, 2006; Hernandez *et al.*, 2006; Giovanelli *et al.*, 2010; Mateo *et al.*, 2010). The use of MAXENT is also appropriate here, given that it does not require true absence data, which are difficult to obtain and often unreliable in tropical regions (Graham *et al.*, 2004; Elith *et al.*, 2010).

We generated three distribution models for each species under different climatic scenarios (current, 6000 and 21,000 years ago). The models were based on climatic variables obtained from WorldClim (Global Climate Data, available at http://www.worldclim.org). The seven variables used matched those used in the generation of forest refugial models by Carnaval & Moritz (2008), namely annual mean temperature, temperature seasonality, mean temperature of the warmest and coldest quarters, annual precipitation and

Table 1 Endemic species used in this study, with details about their range attributes. Occurrence region was based on collection records and literature data. Predicted occurrence area was obtained through species distribution models under current climate. Number of Atlantic forest phytophysiognomies occupied was estimated by plotting records over Brazil's vegetation map. Widely recognized regions of Brazil's coast, and their respective states, are as follows: Northeastern region: Alagoas (AL), Bahia (BA), Paraíba (PB), Pernambuco (PE), Rio Grande do Norte (RN) and Sergipe (SE); Southeastern region: Espírito Santo (ES), Minas Gerais (MG), Rio de Janeiro (RJ) and São Paulo (SP). Southern region: Paraná (PR), Rio Grande do Sul (RS) and Santa Catarina (SC).

	Range characteristics		
Taxon	Occurrence region	Predicted occurrence area (km^2)	No of phytophysiognomies
Araneae			
Phoneutria keyserlingi	Southeast–South (ES, MG, PR, RJ, SC, SP)	661,498	5
Vitalius wacketi	Southeast–South (MG, PR, RJ, SC, SP)	677,850	4
Opiliones			
Ampheres leucopheus	Southeast–South (ES, PR, RJ, SC, SP)	246,162	5
Pristocnemis pustulatus	Southeast–South (MG, PR, RJ, SP)	346,215	5
Scorpiones			
Tityus brazilae	Northeast–Southeast (AL, BA, ES, PE, SE)	181,934	6
Tityus costatus	Northeast–Southeast–south (BA, ES, MG, PR, RJ, RS, SC, SP)	1,380,287	9
Amphibia			
Dendropsophus elegans	Northeast–Southeast–south (AL, BA, ES, MG, PB, PE, PR, RJ, SC, SE, SP)	1,618,279	11
Haddadus binotatus	Northeast–Southeast–south (BA, ES, MG, PR, RJ, RS, SC, SP)	1,205,178	7
Aves			
Phylloscartes kronei	Southeast–South (PR, RS, SC, SP)	171,955	5
Ramphocelus bresilius	Northeast–Southeast–south (AL, BA, ES, MG, PB, PE, PR, RJ, SC, SP)	1,005,030	10
Squamata			
Enyalius catenatus	Northeast–Southeast (AL, BA, ES, MG, PB, PE, RN)	1,149,405	7
Leposoma scincoides	Northeast–Southeast (BA, ES, MG, RJ)	203,222	8
Mammalia			
Euryoryzomys russatus	Southeast–South (BA, ES, MG, PR, RJ, RS, SC, SP)	1,331,081	8
Marmosops incanus	Northeast–Southeast (BA, ES, MG, RJ, SP)	1,446,315	9

precipitation of the driest and wettest quarters (Hijmans *et al.*, 2005). All variables were employed at 30´´ spatial resolution. We allowed MAXENT to randomly select pseudo-absence points within all of Brazil's territory, with the aim of generating more accurate models (Giovanelli *et al.*, 2010; Mateo *et al.*, 2010). Current model accuracy was tested with 20 previously unused presence records randomly selected for each species, through the area under the (ROC) curve, the AUC (Pearson, 2007).

To model the past distribution of the species, we generated distribution using the model of atmospheric general circulation ECHAM3 (Deutsches Klimarechenzentrum Modellbetreuungsgruppe, 1992). To convert continuous models into binary maps of presence and absence, we used a minimum training presence threshold to decrease the chance of omission errors (Pearson, 2007). As in Carnaval & Moritz (2008), refugia were identified through the intersection of the three (current, 6000 and 21,000 years ago) binary models generated per species; areas where a given species was present in all three scenarios were interpreted as regions of climatic stability (refugia; Waltari *et al.*, 2007; Carnaval *et al.*, 2009).

Assessing the impact of taxonomic identity and species-specific range characteristics on the predictive power of forest refugial models

To assess how well the existing Atlantic rain forest refugial model (Carnaval & Moritz, 2008) predicts the location of species-specific refugia, we studied the degree of congruence between predicted forest refugial areas and predicted species refugial areas for the 14 target taxa. To this end, we calculated two metrics (Fig. 1). The first represents the proportion of the species refugial area predicted by the forest refugial model (referred to as the percentage of inclusion). It was calculated as the ratio of the species refugial area predicted by the forest refugial model to the total refugial area of the species. The second metrics represents the proportion of the forest refugial area filled by the species refugial model (referred to as the percentage of filling); it was calculated as the ratio of the species refugial area predicted by the forest refugial model to the total forest refugial area (Fig. 1). Predictive power of forest refugia was interpreted as highest when both filling and inclusion were high. High inclusion and low filling indicate that forest refugia encompass species refugia yet overestimate their size. This result suggests that the forest model is unable to capture lower-order environmental features that limit the range of the species within the biome. High filling and low inclusion indicate that the forest refugia underestimate species refugia. This result suggests that the forest model fails to represent the entire range of environmental conditions that enable species presence. For both metrics, we used the refugial model according to the broader definition of the Atlantic rain forest as per Carnaval & Moritz (2008).

We explored possible impacts of species-specific range characteristics on model inclusion and filling such as the geographic region occupied by the species of interest (southern, Southeastern or Northeastern Brazilian forests), range size (as given by MAXENT's species distribution model) and the number of phytophysiognomies occupied by the species (as demonstrated by plotting 50 random occurrence points onto Brazil's vegetation map; Table 1). To test whether the attributes influence the predictive power of the forest refugial model, we performed two analyses of covariance (ANCOVA), one for each response variable (percentage of inclusion and filling). Because the data of the predictor variables were the

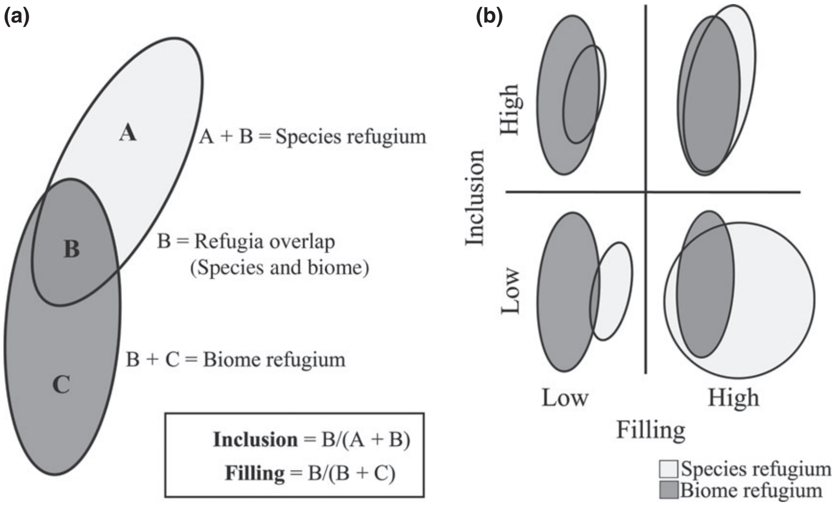

Figure 1 Measuring how well forest refugial models predict species refugia: (a) calculating the percentage of inclusion, which represents how much species refugial models are contained within forest refugial models, and the percentage of filling, which represents how much the species refugial models fill the forest refugial model; (b) different possible outcomes in studies of inclusion and filling (see text).

same, we followed the Bonferroni procedure (Quinn & Keough, 2002) to reduce the significance level of each test to 0.025. Next, we did a planned comparison (contrast) to investigate more precisely the existence of differences between the treatments in the categorical predictor variable (occurrence region of the species). The contrast was intended to compare the predictive power for species occurring in [Northeastern and Southeastern Brazil] versus [Southeastern and southern Brazil] and [Northeastern, Southeastern and southern Brazil, that is, widespread Atlantic forest taxa] versus [Southeastern and southern Brazil] (Table 1). These tests were performed using the STATISTICA software (v 7.0; StatSoft, Inc., Tulsa, OK, USA).

To analyse the influence of taxonomic identity on model inclusion and filling, we constructed a phylogeny of the 14 target species in MESQUITE v 2.74 (http://mesquiteproject.org) (Figure S1), respecting the placement of taxonomic groups proposed by morphological and molecular data (Eernise & Peterson, 2004; Rowe, 2004; Wheeler *et al.*, 2004). We assumed an ultrametric tree in the absence of more precise information (Diniz-Filho, 2000) and used the number of nodes between each pair of species as a proxy for minimum taxonomic distance between them. To test whether taxonomic identity influences how well the forest refugial model predicts species-specific refugia, we performed two Mantel correlation tests (Diniz-Filho, 2000; McCune & Grace, 2002). We built three dissimilarity matrices: (1) taxonomic distance, (2) differences in the percentage of inclusion, and (3) differences in the percentage of filling, and performed two tests of correlation between the matrices (1 vs. 2 and 1 vs. 3) in R (v 2.12.1-R; http://www.r-project.org/). Statistical significance of the correlation was tested after 10,000 permutations. Because we used the same taxonomic distance matrix in both tests, we followed the Bonferroni procedure (Quinn & Keough, 2002) to reduce the significance level of each test to 0.025.

We analysed whether the metrics of predictive power of the biome refugial model (percentage of inclusion and filling) captured different properties of the model by assessing the correlation between them through a Pearson correlation test. We did this test using the STATISTICA software (v 7.0) and assuming a significance level of 0.05.

RESULTS

All species distribution models generated under current climate showed high levels of accuracy, with AUC values ranging between 0.948 and 0.995 (Swets, 1988). Thresholded models denoting presence and absence for each species and climatic scenario are seen in Figures S2–S4. Current distribution models are generally compatible with expert knowledge about the actual distribution of the species, except for the predicted Amazonian range of *Enyalius catenatus* and the overpredictions in Brazil's Midwest region observed in half of the species (*Tityus costatus*, *Dendropsophus elegans*, *Haddadus binotatus*, *Ramphocelus bresilius*, *Enyalius catenatus*, *Euryoryzomys russatus* and *Marmosops incanus*). Historically stable areas (refugial areas) estimated through overlap of predictive models across the three climate scenarios were clearly different across species (Fig. 2). The taxa can be described by the geographic concentration of refugial areas: Northeastern Brazil (*Tityus brazilae* and *Leposoma scincoides*), Southeastern Brazil (*Phoneutria keyserlingi*, *Vitalius wacketi*, *Ampheres leucopheus*, *Pristocnemis pustulatus* and *Phylloscartes kronei)* or both (*Tityus costatus*, *Dendropsophus elegans*, *Haddadus binotatus*, *Ramphocelus bresilius*, *Enyalius catenatus*, *Euryoryzomys russatus* and *Marmosops incanus*).

Taken together, models of species-specific distributions identified five major refugial areas (two large and three small-sized) in the Atlantic rain forest (Fig. 2): a large refugium from northern Espírito Santo to northern coastal Bahia (*Tityus brazilae*, *Tityus costatus*, *Dendropsophus elegans*, *Haddadus binotatus*, *Ramphocelus bresilius*, *Enyalius catenatus*, *Leposoma scincoides* and *Marmosops incanus*), a large refugium in the Southeastern region, including southern Rio de Janeiro, Northeastern São Paulo and Southeastern Minas Gerais (*Ampheres leucopheus*, *Pristocnemis pustulatus*, *Phoneutria keyserlingi*, *Vitalius wacketi*, *Tityus costatus*, *Dendropsophus elegans*, *Haddadus binotatus*, *Phylloscartes kronei*, *Ramphocelus bresilius*, *Euryoryzomys russatus* and *Marmosops incanus*), one small area in coastal Alagoas and Pernambuco (*Dendropsophus elegans*, *Enyalius catenatus* and *Marmosops incanus*), one small area in the Chapada Diamantina, interior Bahia (*Tityus brazilae*, *Tityus costatus*, *Dendropsophus elegans*, *Haddadus binotatus*, *Ramphocelus bresilius*, *Enyalius catenatus*, *Leposoma scincoides* and *Marmosops incanus*) and a last one small area in Northeastern Mato Grosso do Sul (*Tityus costatus*, *Dendropsophus elegans*, *Haddadus binotatus*, *Ramphocelus bresilius*, *Enyalius catenatus*, *Euryoryzomys russatus* and *Marmosops incanus*).

Percentage of inclusion of species refugia within the published biome (forest) refugia ranged from 0% (*Phylloscartes kronei*) to 83.1% (*Leposoma scincoides*). Percentage of filling ranged from 0% (*Phylloscartes kronei*) to 80.6% (*Dendropsophus elegans*). Values of inclusion and filling were not simultaneously high for any species. These two variables represent different predictive properties of the biome refugial model because they are not correlated (Pearson correlation, $r = 0.44$, $P = 0.11$). Percentage of inclusion was not influenced by the taxonomic identity (Mantel, $r = 0.084$, $P = 0.151$) nor by species range attributes (ANCOVA, $F_{1,9} = 1.27$, $P = 0.29$, Fig. 3). Percentage of filling was not influenced by the taxonomic identity (Mantel, $r = 0.133$, $P = 0.094$), but was influenced by the range attributes of the species (ANCOVA, $F_{1,9} = 45.06$, $P < 0.001$, Fig. 3). After detailing the influence of range attributes, we found that the percentage of filling was not influenced by the number of phytophysiognomies occupied by the species (ANCOVA, $F_{1,9} = 0.27$, $P = 0.613$), but it was significantly influenced by the predicted area of occurrence (range size; ANCOVA, $F_{1,9} = 19.65$, $P = 0.002$); habitat model filling was significantly higher in widely

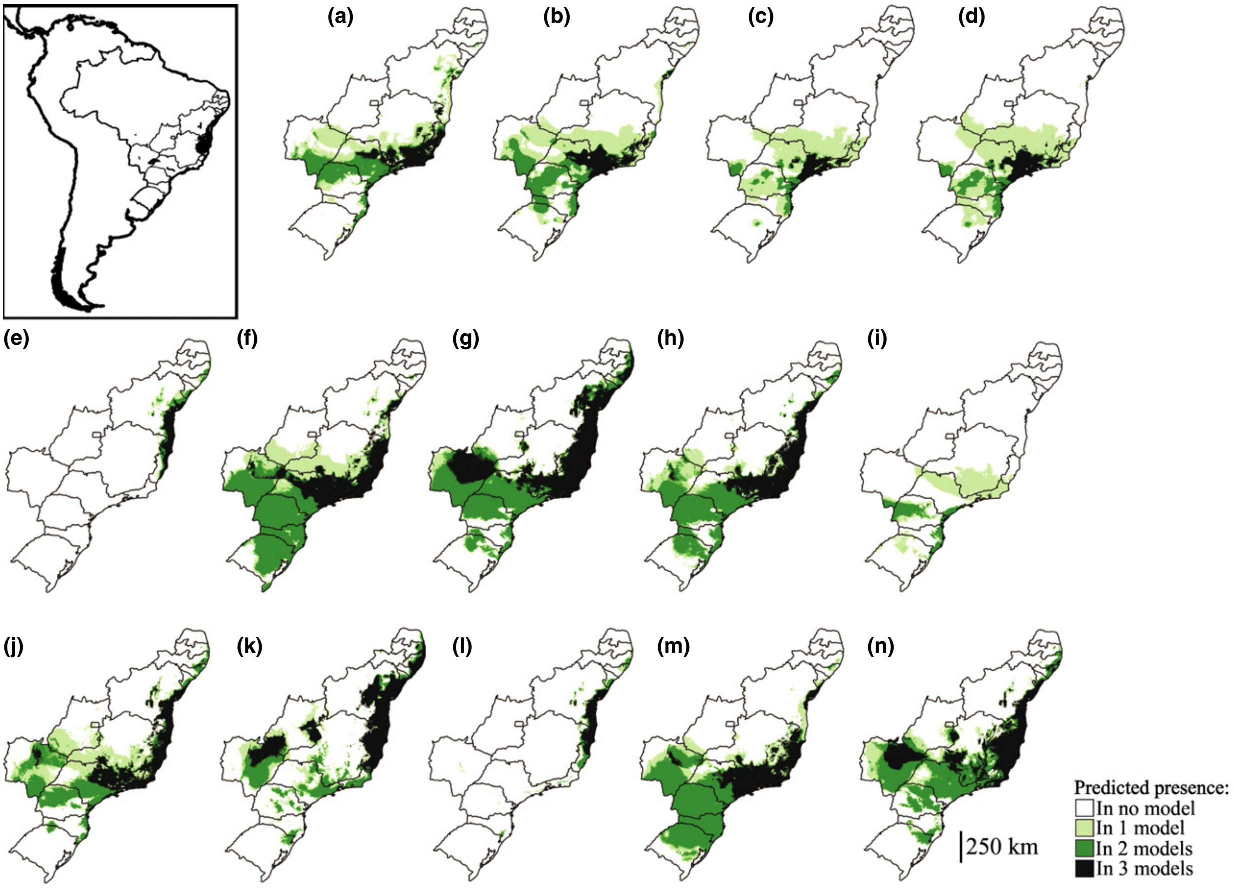

Figure 2 Location of refugial areas for 14 Atlantic rain forest endemic animals. Map in upper left corner provides location of the study area in South America and the distribution of refugial areas proposed by Carnaval & Moritz (2008). Figures indicate refugial areas for 14 species: (a) *Phoneutria keyserlingi*, (b) *Vitalius wacketi*, (c) *Ampheres leucopheus*, (d) *Pristocnemis pustulatus*, (e) *Tityus brazilae*, (f) *Tityus costatus*, (g) *Dendropsophus elegans*, (h) *Haddadus binotatus*, (i) *Phylloscartes kronei*, (j) *Ramphocelus bresilius*, (k) *Enyalius catenatus*, (l) *Leposoma scincoides*, (m) *Euryoryzomys russatus* and (n) *Marmosops incanus*. Colours represent the overlap of models generated under three climatic scenarios (current, 6000 and 21,000 years ago).

distributed species. Geographic region of occurrence also impacted the percentage of filling (ANCOVA, $F_{2,9} = 13.81$, $P = 0.002$); filling was higher in species occurring in both Northeastern and Southeastern regions relative to those occurring in Southeastern and southern regions alone (Contrast, $t = 3.71$, $P = 0.003$). No significant differences in the percentage of filling is observed between species in Northeastern-Southeastern-Southern regions versus species in Southeastern-Southern regions only (Contrast, $t = -0.92$, $P = 0.38$) (Table 1, Fig. 3).

DISCUSSION

Location of refugia

Based on the distribution models of 14 Atlantic rain forest endemic species, we predict the location of five refugial areas, three of them highly coincident with biome (forest) refugial areas proposed by Carnaval & Moritz (2008). The latter are the large Bahia refugium and smaller refugia in Chapada Diamantina and the coast of Alagoas and Pernambuco. However, our models repeatedly pointed to two additional species refugia that were not recognized in Carnaval & Moritz's (2008) forest refugial model: a large refugium in Southeastern Brazil and a small refugium in Northeastern Mato Grosso do Sul. The existence of a Southeastern refugia had been suggested by previous models based on climatic and vegetation data (Ab'Sáber, 1977; Jackson, 1978), as well as species diversity data for butterflies (Brown, 1982), scorpions (Lourenço, 1987) and plants (Prance, 1982). A refugium in Northeastern Mato Grosso do Sul has also been indicated in previous models, based on the diversity data of scorpions (Lourenço, 1987) and butterflies (Brown, 1982). These areas, especially the Southeast coast, are known to show high levels of species richness and endemism for different taxa (Soderstrom *et al.*, 1988; Costa *et al.*, 2000; da Silva *et al.*, 2004; Pinto-da-Rocha *et al.*, 2005) and records of higher genetic diversity in populations of endemic animals and plants (Mustrangi & Patton, 1997; Leite, 2003; Carnaval & Moritz, 2008), classical biogeographic implications of the refugial

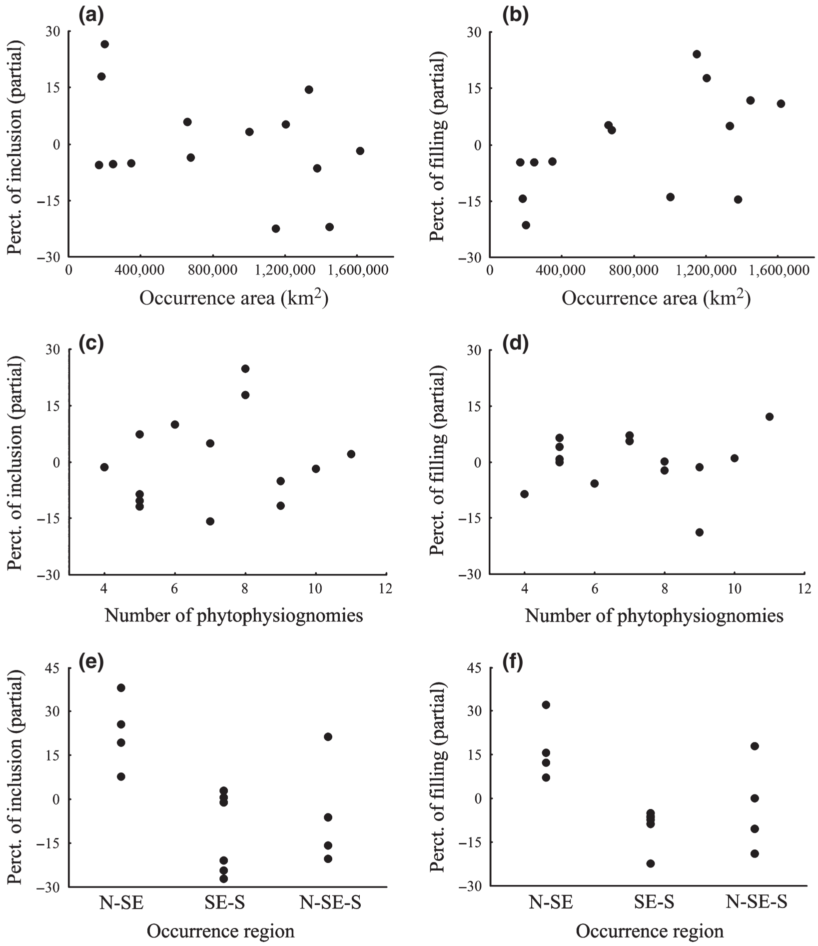

Figure 3 Partial graphs depicting the relationships between the percentage of inclusion (left column) and percentage of filling (right column) with three predictor variables: species occurrence area (a and b), number of phytophysiognomies occupied by the species (c and d) and occurrence region in the Atlantic rain forest (e and f). N–SE=Northeastern–Southeast; SE–S=Southeastern-South; and N–SE–S=Northeastern-Southeastern-South (Table 1).

forest formation. The high species diversity of these regions, added to the fact that they had been proposed as refugia based on different methodological approaches, provides support to the view of these areas as Atlantic rain forest refugia.

The fact that these two areas have not been indicated as refugia in the Carnaval & Moritz (2008) model may be related to the limitation of a methodological procedure adopted by these authors. In predicting the Atlantic rain forest refugial areas, the authors used two modelling methods (MAXENT and BIOCLIM), two biome definitions and three climatic scenarios, and the refugial areas are those indicated as biome presence in all models. Therefore, refugial areas would be indicated basically by the more restrictive models. The projections of the biome distribution to 21,000 years ago using BIOCLIM (for the broader and narrower biome definition) were quite restrictive, and this is the only projection in which the refugial areas in Northeastern Mato Grosso do Sul and the Southeastern Brazil were not predicted (Fig. 2 in Carnaval & Moritz, 2008). BIOCLIM has been identified as providing the lowest performance in recent model comparisons (Elith *et al.*, 2006; Hernandez *et al.*, 2006), especially in the face of restriction excesses and extrapolation. Thus, perhaps these areas have been Pleistocene refugia of the biome, yet masked by limitations of the procedure used by the authors. This can be tested through new biome refugial models built with better performance algorithms.

Interspecific variation of the predictive power of the existing Atlantic rain forest refugial model

The ability of the currently available Atlantic forest refugial model (Carnaval & Moritz, 2008) to predict refugial sites specific to endemic animals varied widely between species. Differences in percentages of inclusion and filling, metrics that capture the predictive power of the biome refugial model, were not influenced by the taxonomic identity of the species modelled. This effect was expected because of the relationship between the taxonomic identity and recognized characteristics that influence the accuracy of predictive models (McPherson & Jetz, 2007), such as dispersal ability and trophic level (Fielding & Bell, 1997; Huntley *et al.*, 2004). However, our negative result could be explained by the fact that the biome refugial model has been formulated based on climatic variables that widely influence the endemic biota (Carnaval & Moritz, 2008), but do so differentially and are unrelated to phylogenetic signal.

We expected to find a relationship between the predictive power of the biome refugial model and species-specific range attributes because the Carnaval–Moritz forest model has shown different predictive capabilities for organisms belonging to the same taxonomic group in previous studies (Carnaval *et al.*, 2009 and Thomé *et al.*, 2010 for frogs; Cabanne *et al.*, 2008 and Mata *et al.*, 2009 for birds). However, our data demonstrate that the percentage of inclusion of the species refugial model in the biome refugial model was not influenced by range attributes. This means that the Atlantic rain forest refugial model can be applied to species with different range characteristics without creating a bias in the predictive power informed by inclusion. We, nonetheless, suggest further investigation of the influence of biological traits on the percentage of inclusion, such as the physiological limits of species (McPherson & Jetz, 2007).

In agreement with our predictions, the percentage of filling of the biome refugia by species-specific refugia was significantly influenced by species range attributes, particularly the geographic (thus environmental) space occupied by the target taxa. Our data indicate that the predictive power of the biome refugial model is higher for species that are most widely distributed; species with higher distribution amplitude will fill more of the biome refugia, which was expected for a sampling effect. The data indicate that filling is not influenced by the number of phytophysiognomies occupied by the species, that is, habitat fidelity did not influence the predictive power of the biome refugial model. Because the biome model that we use to calculate the predictive power was generated from data of all phytophysiognomies (Carnaval & Moritz, 2008), we expected that the percentage of filling would be higher for species that use more phytophysiognomies, a pattern not found in our results. The available refugial model can thus be used for both generalist and specialist species, in relation to phytophysiognomies, without any directional effect on its predictive ability.

Our results also revealed that the percentage of filling is greater for species with occurrence in the Northeast-Southeast regions, as compared to organisms that occur in the Southeast-South and Northeast-Southeast-South regions. This result corroborates speculation in the literature that the predictive power of the Atlantic rain forest refugial model is weaker for species with restricted occurrence in the colder, Southeast-South portion of the biome (Costa *et al.*, 2000; Grazziotin *et al.*, 2006; Cabanne *et al.*, 2008; Thomé *et al.*, 2010). This result is probably related to the lack, in the currently available forest refuge model, of a larger refugial area in the Southeast Brazil – something strongly contradicted by paleoecological and diversity data (*e.g.* Ab'Sáber, 1977; Brown, 1982; Lourenço, 1987).

Our general results demonstrate that species-specific and the available forest refugial models cannot be used interchangeably across a large set of species, which can explain the mixed support for the proposed location of the Carnaval & Moritz (2008) forest refugial areas based on subsequent phylogeographic studies of distinct taxa. The power of the Brazilian Atlantic forest refugial model to predict the species-specific refuges is substantially different across species, influenced by range attributes. Independent evidence of the existence of species-specific refugial areas in Southeastern Brazil suggests that the Carnaval & Moritz (2008) model can be improved. Our results restrict the predictive power of the existing model of refugia in the Brazilian Atlantic forest and advance in the understanding about their limits of applicability. We expect that the framework here explored will prove useful to interpret models of diversity patterns in other similar biological systems.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Number of records obtained for each species, with sources of information.

Table S1 Species occurrence records used to generate the distribution models.

Figure S1 A scheme of the phylogenetic relationship between the species of this study. This scheme was used to calculate the taxonomic distance by counting the number of nodes between each pair of species. This topology was based on the morphological and molecular phylogeny of the higher taxonomic categories.

Figure S2 The predicted occurrence area for the 14 species of this study for the current climatic scenario. In the upper left, a map of South America showing Brazil (gray) and the distribution of the original Atlantic Rainforest (black).

Figure S3 The predicted occurrence area for the 14 species of this study for the current climatic scenario. In the upper left, a map of South America showing Brazil (gray) and the distribution of the original Atlantic Rainforest (black).

Figure S4 The predicted occurrence area for the 14 species of this study for the palaeoclimatic scenario of 21,000 years ago. In the upper left, a map of South America showing Brazil (gray) and the distribution of the original Atlantic Rainforest (black).

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