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ORIGINAL ARTICLE

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Assessing how habitat loss restricts the geographic range of Neotropical anurans

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Abstract Habitat loss and fragmentation exert unquestionable negative effects in a wide range of taxa on both regional and local scales. However, there is a debate over whether habitat change impacts geographic species distribution. We assess how habitat loss restricts large-scale species distribution on a geographic scale for four South American anurans that are known to occur in well conserved habitats, yet which are absent in others that are close by and more degraded. We used occurrence records of each species in Brazil and performed different modeling algorithms to compare ensemble distribution models generated by two different sets of predictors: a climate-only versus a climate-habitat procedure. We found that the distribution area predicted by the climate-only procedure was larger than that of the climate-habitat procedure for all species. The areas not predicted by the climate-habitat but predicted by the climate-only procedure for all species are commonly located in inland areas in southeastern Brazil, which coincides with areas that have suffered the most from habitat loss in the country. Plotting the predictions against well-surveyed areas where the species have not been recorded, we found evidence that habitat loss may have restricted the current geographic ranges of *Hypsiboas faber* and *Rhinella ornata*. Finally, modeling approaches incorporating habitat landscape metrics, particularly for habitat-specialist species, may be a helpful tool for identifying areas that harbored these species before deforestation took place.

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Introduction

The loss and fragmentation of natural habitats are linked processes that are invariably destructive to biodiversity. These processes result in reduced population sizes or local extinctions due to removal of natural habitat, increased edge effects, isolation of natural populations, and an influx of individuals from altered habitats (Laurance and Bierregaard 1997; Bennett and Saunders 2011). South America has suffered from some of the most intense habitat loss in the world (Whitmore 1997). Two of the most highly impacted areas on the continent are the Atlantic Forest and Cerrado hotspots, which are largely found within Brazil's borders. These areas are distinguished by their high levels of biodiversity and endemism, yet they are highly threatened by human activities (Mittermeier et al. 2004).

Many previous studies evaluating the effects of habitat loss and degradation in the Atlantic Forest and Cerrado hotspots have focused on regional or local scales. For instance, recent studies have demonstrated that human-related habitat alterations influence the patterns of species distribution of several organisms, in which a decreased number of species occurring within an impacted habitat is a general common pattern in specific geographic locations or conservation units (da Silva et al. 2012; Dodonov et al. 2013; Lion et al. 2014).

Although human-induced habitat change generally restricts species distributions to a given region or location, the extent to which the effects of habitat loss constrain species distributions on a broad scale (i.e., the geographic limits of species) remain poorly explored in the literature (e.g., Thuiller et al. 2004; Luoto et al. 2007; Reino et al. 2013). Moreover, it is still debated whether habitat loss and fragmentation impact species distributions on a biogeographic scale. For instance, Triviño et al. (2011) demonstrated that climate variables are sometimes sufficient for predicting a species' range, and that vegetation can help to improve model predictions, but that landscape configurations cannot. Other authors, however, found that habitat loss is more important than climate (Warren et al. 2001) or that it contributes significantly to model predictions of the distribution of habitat specialist species (Reino et al. 2013). Since organisms from different species may exhibit different ecological features to accommodate to changes in habitat, and thus respond differently to habitat loss and degradation processes, the decision over whether to include specific non-climatic predictors when modeling geographic species distributions requires case-specific considerations based on the auto-ecology of the species (Triviño et al. 2011).

Among the wide range of taxa affected by habitat loss and fragmentation (e.g., Laurance and Bierregaard 1997), amphibians are severely affected due to their physiological characteristics (skin permeability and cutaneous gas exchange) and to the life cycle aspects of the group (dependence on aquatic and terrestrial habitats during their life; Wells 2007). Amphibians can be directly affected by anthropogenic habitat changes that result in the loss of natural habitats; some amphibian declines or even local extinctions have been attributed to the habitat loss process (Eterovick et al. 2005). Additionally, indirect effects of human-induced habitat alterations, such as increased edge effects and disconnection between aquatic and terrestrial habitats, have also been associated with declines in amphibian populations (Cushman 2006; Becker et al. 2007). The mechanisms behind habitat alteration processes most commonly involve: (a) the increased risk that pond/stream-dwelling organisms face during breeding migration across disturbed environments located between aquatic and terrestrial habitats (Becker et al. 2010). In this case, organisms are mainly sensitive to habitat loss and fragmentation because they are forced to search for breeding sites surrounded by an inhospitable matrix (Haddad and Prado 2005; Becker et al. 2007; Dixo and Metzger 2010), and; (b) decreased air humidity, which makes the environment unfavorable for species that depend on humid forest microhabitats (Haddad and Prado 2005).

In the present study, we want to explore the extent to which habitat loss influences the species distribution and when it culminates in a total exclusion of the species in a given area, thus redefining its geographic limits. Then, we selected four anuran amphibians that are known to predominantly occur in pristine habitats of the Atlantic Forest and Cerrado hotspots (Brasileiro et al. 2005; Santos et al. 2009; Brassaloti et al. 2010; Maffei et al. 2011), but alternatively have not been recorded in some intensively impacted areas relatively close to preserved ones (Vasconcelos and Rossa-Feres 2005; Santos et al. 2007; Rossa-Feres et al. 2012). Santos et al. (2009) emphasized that the four anurans selected may have been affected by habitat loss in one of the most impacted Brazilian areas, an area which has experienced land conversions to agricultural and pasture systems. Hence, we want to check if modeled predictions detect climatically suitable areas (climate-only modeling approach) for the species in highly devastated areas where the species have not been recorded. On the other hand, we hypothesize that a modeling approach implementing habitat loss information throughout the studied area (climate-habitat modeling) will generate more concise species predictions due to the negative effects of this variable on the four habitat-dependent species (Warren et al. 2001; Luoto et al. 2007; Reino et al. 2013). We also expect that the occurrence areas that were not predicted by the climate-habitat models but which were predicted by the climate-only procedure will coincide with the most heavily impacted areas where the species are absent.

Methods

Species studied and occurrence records

We selected four anuran species that are associated with forested habitats (or with their borders)—either with different forest physiognomies in the Atlantic Forest or with gallery forests along streams and rivers in the Cerrado (Brasileiro et al. 2005; Santos et al. 2009; Brassaloti et al. 2010; Maffei et al. 2011). *Hypsiboas faber* and *Itapotihyla langsdorffii* have wide geographic ranges throughout the different eco-regions in the Atlantic Forest (moist forests or semideciduous/deciduous forests; see Vasconcelos et al. 2014). However, they also occur in gallery forests within the Cerrado domain, which ranges from northeastern to southern Brazil, southeastern Paraguay, and in the Argentinean province of Misiones (Frost 2014). *Hypsiboas lundii* is most commonly associated with gallery forests of the Cerrado in central-eastern and southeastern Brazil (Frost 2014; IUCN 2014). *Rhinella ornata* has a smaller range than the other species; it is most commonly found in the Atlantic forest in southeastern and part of southern Brazil (e.g., moist and semideciduous/deciduous forests), but can also be found in gallery forests of the Cerrado in southeastern Brazil (Frost 2014).

We gathered point occurrence data on each species from open-access digital databases (the Global Biodiversity Information Facility, or GBIF; Yesson et al. 2007; the SpeciesLink project; http://splink.cria.org.br). Due to biased records in southeastern Brazil (Vasconcelos and Nascimento 2014), we also obtained data from the amphibian collection at the Federal University of Bahia (UFBA) on species with wider distributions in northeastern Brazil. We followed the procedures used by Vasconcelos and Nascimento (2014) (see also Araújo and Guisan 2006) and filtered the raw data in order to remove duplicate, erroneous, and/or imprecise point occurrences (coordinates assigned to municipalities). We obtained a total of 148 different occurrence records to use in the modeling process for *H. faber*, 58 to use in the modeling process for *H. lundii*, 56 to use in the modeling process for *I. langsdorffii*, and 88 to use in the modeling process for *R. ornata*.

Modeling procedure

We used six modeling methods to generate the distribution models (e.g., Nix 1986; Stockwell and Peters 1999; Elith et al. 2006; Giovanelli et al. 2010; Muñoz et al. 2011; Vasconcelos 2014): the bioclimatic envelope algorithm (BIOCLIM); the climate space model (CSM); the envelope score (ES); environmental distance (ED); the genetic algorithm for rule-set production with a new openModeller implementation (OM-GARP); and support vector machines (SVM). These methods can essentially be classified into two types (sensu Rangel and Loyola 2012): (a) envelope models (BIOCLIM, CSM, ES, and ED), the concepts of which rely on assumptions that are intuitive to any ecologist, thus tending to sacrifice precision and realism for the sake of generality; and (b) machine-learning models (OM-GARP and SVM), which are complex models that maximize their predictive power while minimizing the number of parameters, and which also lack a constraint that would limit the maximum number of parameters or the complexity of the relationship between species occurrence and environmental factors (see details in Rangel and Loyola 2012). Unlike the envelope models, machine-learning models tend to sacrifice realism and generality for the sake of precision (Rangel and Loyola 2012). Although both types have their advantages and limitations (see Rangel and Loyola 2012), there is a consensus in the literature that there is no best method for predicting the presence or absence of species according to environmental variables (Araújo and New 2007; Loyola et al. 2014). Therefore, we use the ensemble of forecasting approach, which has been proven to be more interpretative than a single-model analysis (Loyola et al. 2014), in order to address the inherent differences between the modeling methods (see ahead). Models were run in openModeller 1.1.0 (Muñoz et al. 2011), and parameterizations followed default options. Models were evaluated using the receiver operating characteristic (ROC) curve, whose area under the curve (AUC) ranges from 0 to 1. AUC values of 0.5 represent a model no better than random, whereas a value of 1 indicates perfect model discrimination between presence and absence records (Elith and Burgman 2002; Graham and Hijmans 2006). Therefore, we discarded models with an AUC below 0.75 because they are generally not discriminatory enough to be helpful (Elith and Burgman 2002).

We performed two modeling procedures for each species. First, we applied climate-only modeling (the Ecological Niche Modeling approach, or ENM; Araújo and Peterson 2012; Peterson and Soberón 2012), in which we modeled the climatic suitability of each species as a function of seven climatic variables considered to describe general climatic trends, variation in temperature and precipitation over time, and potential physiological limits for the species (Nix 1986; Vasconcelos et al. 2012), all of which was considered at a spatial resolution of ~ 10 km (Hijmans et al. 2005). The seven climactic variables were annual mean temperature, temperature seasonality, minimum temperature of the coldest month, annual range in temperature, annual precipitation, precipitation seasonality, and precipitation of the warmest quarter. In order to accurately improve the reconstruction of the species distributions, we performed a second procedure using a species distribution modeling approach (SDM; Araújo and Peterson 2012; Peterson and Soberón 2012). Conceptually, the SDM definition must include steps to transform areas estimated from potential (e.g., those obtained from the ENM procedure) to actual. Thus, we included a remnant vegetation layer in addition to the previous seven climatic variables, an approach that will henceforth be referred to as climate-habitat modeling. This remnant vegetation layer was chosen to represent the amount of native habitat that is available for the four anuran species along their distributional ranges. Specifically, this layer contains information on the total native vegetation area (i.e., moist, semideciduous, and/or gallery forests) that remained within the ~ 10 km grid resolution cell after habitat loss as of 2008 (Brazilian Biomass Deforestation Monitoring Project, or PMDBBS, available at http://siscom.ibama.gov.br/monitora_biomas/). The original shapefile was converted into a grid file by the Brazilian National Center for Reptile and Amphibian Research and Conservation (RAN) of the Chico Mendes Institute for Biodiversity Conservation (ICMBIO); the file is available on the ICMBIO portal (http://www.icmbio.gov.br/ran/images/stories/Downloads/grid_perda_vegetacao.zip). Next, we converted the grid file into a raster format for model running (Fig. 1). Though most of the species' geographic range falls within Brazil's borders, the edges of the species' range reach Argentina and Paraguay (with the exception of *H. lundii*). However, we restricted the calibrated area for model running to Brazil, and therefore did not consider species occurrences in the neighboring countries. We are aware that a more complete dataset that considers all known occurrence records is preferable in distribution models (Araújo and Guisan 2006), but the vegetation layer used herein is restricted to Brazil, so we were forced to exclude the records in Argentina and Paraguay. Nonetheless, we believe that the consequences of this omission are minimized by the fact that most of the geographic extent of the studied species falls within Brazil's borders, and that species occurrence in the neighboring countries represents only a small fraction of the species' range.

Ensemble forecasting and final maps

To conciliate the inherent differences between the modeling methods, we obtained consensus maps for each species by generating ensemble forecasts

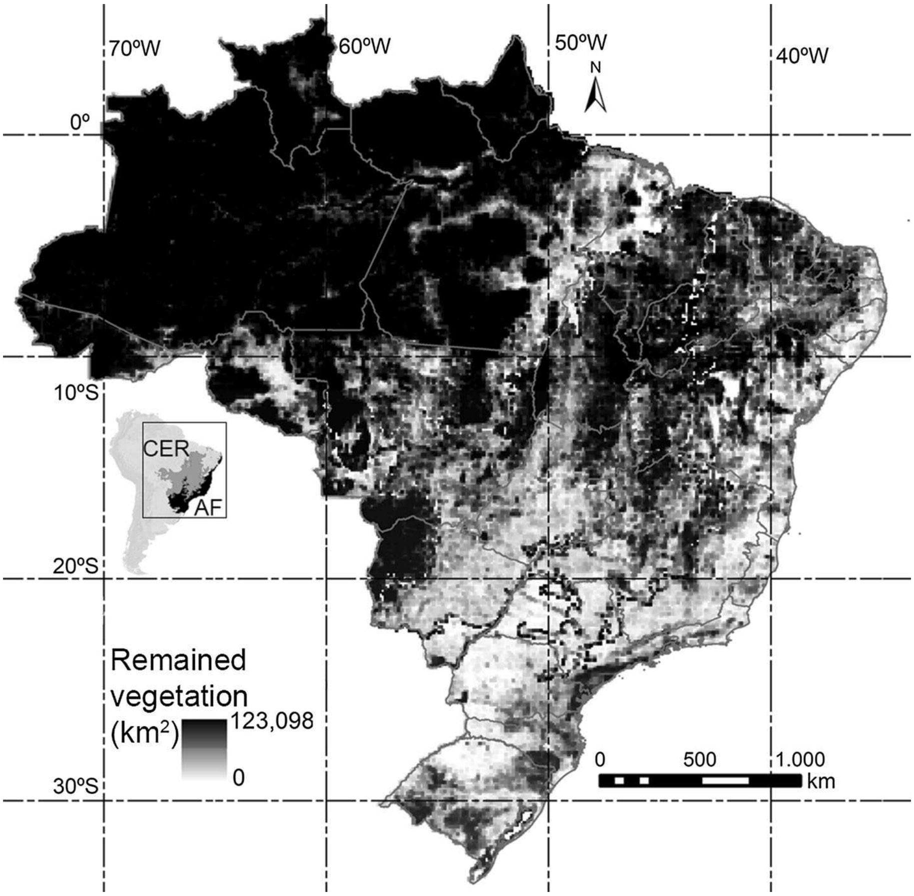

Fig. 1 Map of Brazil showing remaining original vegetation after habitat loss as of 2008 (the Brazilian Biomass Deforestation Monitoring Project, or PMDBBS, available at http://siscom.ibama.gov.br/monitora_biomas/) at a grid resolution of ~ 10 km (modified from the Brazilian National Center for Reptile and Amphibian Research and Conservation, or RAN,of the Chico Mendes Institute for Biodiversity Conservation, or ICMBIO: http://www.icmbio.gov.br/ran/images/stories/Downloads/grid_perda_vegetacao.zip). The hotspots Atlantic Forest (AF) and Cerrado (CER) are highlighted in the smaller South America map

(Araújo and New 2007) that depict the most suitable areas of species occurrence. We created a binary map from each modeling output. The outputs considered the frequency of occurrences higher than 50 % (e.g., Vasconcelos and Nascimento 2016; Loyola et al. 2013). The binary maps were then overlapped; therefore, the final map of each species (separated by the climate-only and climate-habitat procedures) represents a frequency histogram with the number of models forecasting the presence of the species at any given point (Araújo and New 2007). Therefore, each species has a map based on the combination of a maximum of six algorithms or the total number of algorithm predictions with an AUC > 0.75 that remained for the ensemble procedure. Finally, we used ArcGIS 10.1 to calculate the total predicted suitable area for each species and each modeling procedure based on the median forecast (Araújo and New 2007), which meant that the species were considered present in at least half of the models plus one.

Results

Model performance and common patterns among species

All six modeling methods presented overall satisfactory predictions (AUC > 0.75); however, due to low predictive power of the models (AUC ≤ 0.75), BIOCLIM, CSM, and ES were excluded from the *H. faber* predictions, and CSM was excluded from the *I. langsdorffii* predictions (Table 1). The other valid predictions were congruent with the known occurrence records of the four species, though we found either underestimations (e.g., *H. lundii*) or overestimations (e.g., *I. langsdorffii*) in the final models (Fig. 2).

A common pattern found for all species was the decrease in predicted suitable occurrences in the climate-habitat models relative to the climate-only models (Table 2). The losses varied from a magnitude of 2.76 % (*H. faber*) to a magnitude of 10.69 %

Table 1 AUC values (see “Methods”) of the model evaluation of each modeling algorithm (MA) performed for each species and for each modeling procedure (the climate-only approach and the climate-habitat modeling approach, respectively)

MA	*Hypsiboas faber*	*Hypsiboas lundii*	*Itapotihyla langsdorffii*	*Rhinella ornata*
BIOCLIM	0.74, 0.74*	0.80, 0.81	0.84, 0.85	0.90, 0.91
CSM	0.71, 0.70*	0.80, 0.80	0.51, 0.40*	0.84, 0.81
ES	0.74, 0.75*	0.79, 0.80	0.84, 0.84	0.90, 0.91
ED	1.00, 1.00	1.00, 1.00	1.00, 1.00	1.00, 1.00
OM-GARP	0.80, 0.80	0.87, 0.88	0.84, 0.86	0.90, 0.89
SVM	0.90, 0.89	0.89, 0.90	0.96, 0.94	0.94, 0.94

BIOCLIM bioclimatic envelope algorithm; *CSM* climate space model; *ES* envelope score; *ED* environmental distance; *OM-GARP* genetic algorithm for rule-set production with a new openModeller implementation; *SVM* support vector machines. *Asterisk* models with AUC ≤ 0.75 that were discarded

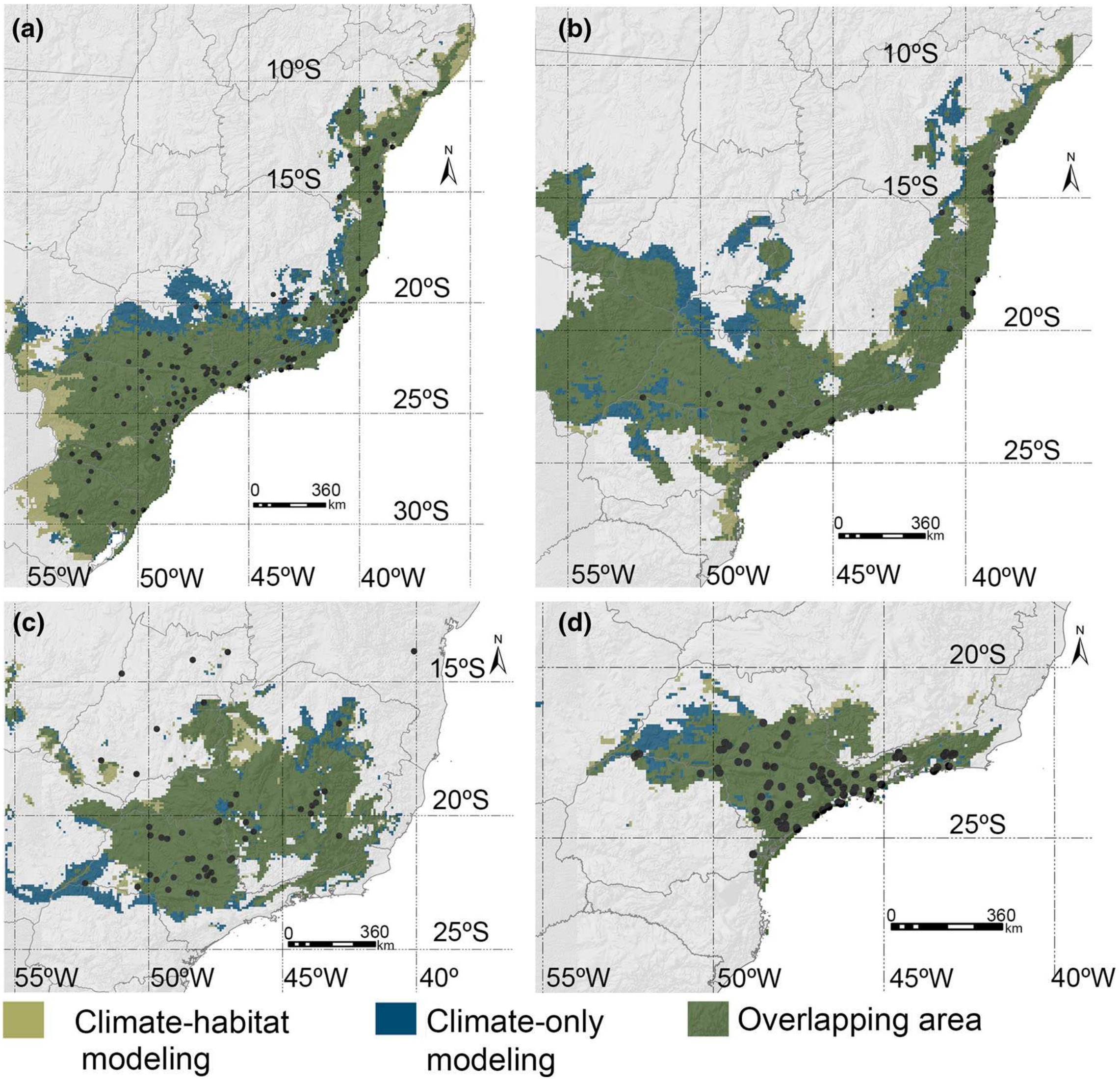

Fig. 2 Presence records and final consensus maps of the modeled distribution of the four anuran species considering the climate-only model, the climate-habitat model, and the overlapping area of both modeling procedures: **a** *Hypsiboas faber*, **b** *Itapotihyla langsdorffii*, **c** *Hypsiboas lundii*, and **c** *Rhinella ornata*

(*I. langsdorffii*), with intermediate values for *R. ornata* (7.50 %) and *H. lundii* (9.81 %). A region that was predicted to have climatically suitable areas for all of the species but which was not considered in the climate-habitat models was inland areas from southeastern Brazil (between latitudes 18 and 24°S and

Table 2 Predicted suitable areas (km^2) considering the final consensus maps for climate-only (C–O) and climate-habitat (C–H) modeling procedures and estimated loss of geographical distribution ranges (the percentage difference between C–O and C–H)

Species	C–O	C–H	Loss (%)
Hypsiboas faber	1,127,068.52	1,095,971.59	2.76
Hypsiboas lundii	641,237.53	578,340.47	9.81
Itapotihyla langsdorffii	1,101,909.70	984,085.13	10.69
Rhinella ornata	251,041.33	232,211.28	7.50

longitudes 49 and 55 °W). These areas are the most degraded regions in Brazil (Figs. 1, 2).

Hypsiboas faber

This species has the largest latitudinal extent of occurrence and, therefore, the largest climatic suitable area predicted (Table 2; Fig. 2). The predicted area ranges from the northeastern Brazil (latitude ca. 8°S), in the Atlantic Forest that extends along the coast to southern Brazil (latitude ca.31°S). The occurrence records and climatically suitable areas at latitudes around 20°S expand southwestward, encompassing areas of semideciduous Atlantic Forest and the Brazilian Cerrado. The climate-habitat model essentially followed the climate-only predictions, but a loss of suitable areas (Table 2) was found in inland Brazilian areas encompassing the western range of the species (Fig. 2). Conversely, gains in suitable areas are predicted in the southwest and extreme north of the species' range (Fig. 2).

Hypsiboas lundii

The distribution of this frog mainly occurs within the Cerrado domain and in transitional areas to the seasonally dry Atlantic forest. The climatically suitable areas are most commonly located between the latitudes 15 and 24ºS and between the longitudes 40 and 54ºW (Fig. 2). The climate-habitat model predicted a loss of 9.81 % of suitable areas relative to the climate-only model (Table 2). The lost areas are mainly located in the northeastern and southwestern portions of the species' range. In the climate-habitat model, new suitable areas were most commonly found in the north, but minor gains were found in the western and southwestern areas of the species' range (Fig. 2).

Itapotihyla langsdorffii

This frog occurs from northeastern Brazil (latitude ca. 12°S) along the Atlantic Forest to southeastern Brazil (latitude ca. 25°S) and westward (up to longitudes ~ 52°W) at latitudes around 20°S, but the climatically suitable areas are found from latitudes ~ 9°S to ~ 27°S and longitudinally from the Atlantic coast to ~ 56ºW (Fig. 2). A large climatically suitable area was predicted in the western region of the species' range, in which no point occurrence is known for the species (Fig. 2). In the climate-habitat model, the predicted distribution was 10.69 % less than the distribution predicted in the climate-only model (Table 2). This loss is mainly found inland, in the western rim of the species' range, but minor losses were also found along the Atlantic coast. Minor gains were minimal compared to the losses and were mainly found along the Atlantic coast (Fig. 2).

Rhinella ornata

This toad has the smallest extent of occurrence among the species. It was most commonly found within the Atlantic Forest domain and in transition zones to the Cerrado in southeastern Brazil (between the latitudes 21 and 26°S and longitudes 43 and 52 °W) (Fig. 2; Table 2). The climatically suitable areas are comprised of the coastal Atlantic Forest and inland areas, but the climate-habitat model predicted a restricted occurrence of the species (at a magnitude of 7.5 %) in areas located in its northwestern extent of occurrence. Minor gains are also expected in some northern areas of the species' range (Table 2; Fig. 2).

Discussion

As expected, we found that a modeling procedure implementing the habitat loss variable generated restricted predictions compared to a climate-only procedure, thus influencing the broad-scale distribution predictions. Therefore, our results provide evidence that the habitat loss process may have effectively restricted broad-scale species distribution in some specific distributional limits.

Hypsiboas faber, *I. langsdorffii*, and *R. ornata* occur in well preserved areas of Atlantic semideciduous forest that are surrounded by landscapes dominated by agricultural and pasture systems (see Santos et al. 2009; Brassaloti et al. 2010). Conversely, these species have not been recorded in areas that have been completely or extensively degraded (i.e., areas with few to no natural remnants), such as those considered to be the areas most highly impacted by agricultural expansion in the state of São Paulo (southeastern Brazil) during the last century (Bernarde and Kokubum 1999; IPT 2000; Vasconcelos and Rossa-Feres 2005; Santos et al. 2007; Rossa-Feres et al. 2012). Because the earliest information on anuran species in the region dates from the 1960s (Vizotto 1967), we do not know if these species occurred in these areas before the deforestation began in the 1920s, during the early colonization period (IPT 2000; Santos et al. 2007). Thus, it is difficult to determine whether a species' absence in a given location is a consequence of habitat loss or a reflection of natural biogeographic patterns. The scenario that considers the habitat loss process restricting the species distribution is more evident for *H. faber* because the climate-only model alone (but not the climate-habitat model) predicted climatically suitable areas at most of the locations surveyed by Bernarde and Kokubum (1999), Vasconcelos and Rossa-Feres (2005), Santos et al. (2007), and Rossa-Feres et al. (2012) (Fig. 3a), where these species have not been recorded. The same explanation may partially be the case of *R. ornata*, a species which is absent from the same locations. These locations are slightly outside or within a narrow predicted occurrence area generated by the models (Fig. 3b). However, other areas in the same region were only predicted as climatically suitable for *R. ornata* (western climate-only predicted areas; Fig. 3b), but no occurrence record is known for the species in those areas. Since these areas have been historically less explored by herpetologists (see Rossa-Feres et al. 2011), only future field expeditions in the area to determine the presence or absence of the species will allow us to infer whether habitat loss influenced the current pattern of species distribution. The predictions for *I. langsdorffii* are too complex to evaluate and may involve factors other than climate and vegetation variables constraining species distribution. For instance, the aforementioned locations fall within some suitable areas predicted by both modeling procedures, but this frog has not been detected in extensive field work in the region (Bernarde and Kokubum 1999; Vasconcelos and Rossa-Feres 2005; Santos et al. 2007; Rossa-Feres et al. 2012).

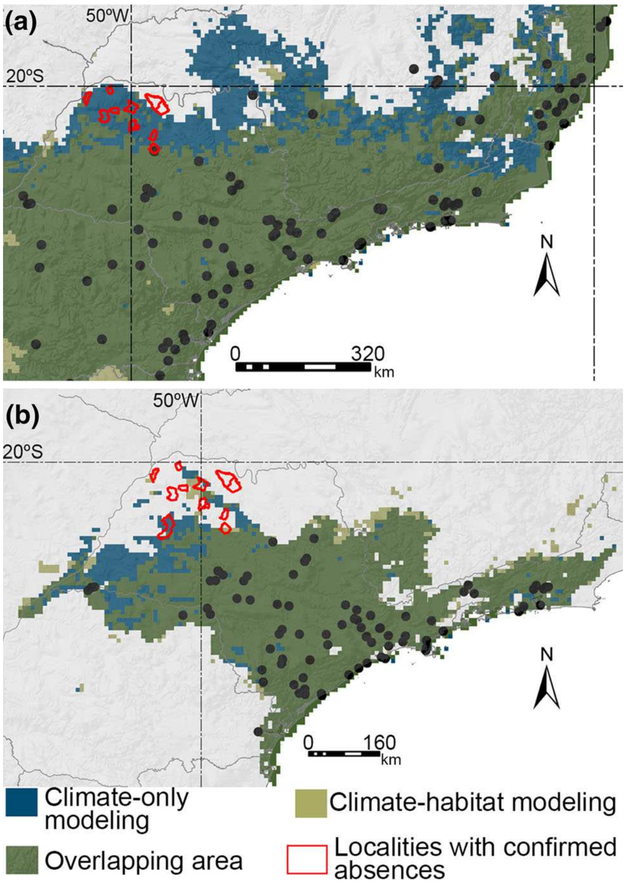

Fig. 3 Locations with absence records surveyed by Bernarde and Kokubum (1999); Vasconcelos and Rossa-Feres (2005); Santos et al. (2007), and Rossa-Feres et al. (2012) on the final consensus maps of the modeled distributions of **a** *Hypsiboas faber* and **b** *Rhinella ornata*

As a common limitation found in climate-only modeling processes in the literature, our climate-habitat procedure also generated underestimations and overestimations of species distribution (Franklin 2010). The most evident cases, for instance, are (a) the false-positive predictions of *I. langsdorffii* in the western predicted area, which includes areas where the species had never been recorded and which were either close to (Bernarde and Kokubum 1999; Vasconcelos and Rossa-Feres 2005; Santos et al. 2007; Rossa-Feres et al. 2012) or far from (Uetanabaro et al. 2007) the known occurrence records; and (b) the false-negative predictions of *H. lundii* in some northern areas where occurrence records are known for the species (Fig. 2). The modeling procedures used here are based exclusively or primarily on climatic variables, which means that the resulting models are unable to predict presences or absences generated by species' evolutionary history or dispersal limitations. This factor may therefore generate commission or omission errors (Graham and Hijmans 2006; Pineda and Lobo 2009).

Another fact that may limit the interpretation of the modeling outputs is that non-climatic factors are likely to restrict species distributions on different spatial scales (Willis and Whittaker 2002), in which biotic interactions, habitat loss, and other landscape features have major influences over species distribution on finer scales (da Silva et al. 2012; Reino et al. 2013 and references therein). Hence, the broad-scale distribution maps generated herein may not be able to accurately evaluate small-scale species distribution. On the one hand, both modeling approaches have correctly predicted the presence of *H. lundii* in a large forest remnant (Santos et al. 2009; see the westernmost record of the species in Fig. 2), which is surrounded by an agricultural landscape where the species has neither been recorded nor predicted by the climate-habitat models. On the other hand, both climate-only and climate-habitat models have predicted the occurrence of *H. lundii* in an intensively devastated area where the species is not known to occur (Vasconcelos and Rossa-Feres 2005). However, the authors (TS Vasconcelos and DC Rossa-Feres, unpublished data) eventually found this species in nearby remnants of a small gallery forest. Therefore, because the models predicted species presence in some cells in which we know that the species is truly absent, it is clear that some habitat loss information was not captured during model building due to different analytical scales and to the fact that some species may be more sensitive to habitat loss and fragmentation than others (e.g., Dixo and Metzger 2010; Triviño et al. 2011).

In conclusion, when extensive historical species records are not available, climate-only predicted areas can be hypothetically considered to be areas where the species could have occurred before habitat loss took place. When it comes to all of the anurans studied herein, most of these predicted areas are located in Brazil's southeastern and southern regions (Figs. 1, 2), which are considered to be the regions in the country that have been most highly impacted by habitat destruction over the last century (IPT 2000). Although there is a debate among ecologists as to whether habitat degradation effectively influences species distributions on a geographical scale (see Reino et al. 2013), we have found evidence that habitat loss has restricted the current geographic ranges of some species, as might be the case for *H. faber* and *R. ornata*. However, further field work is needed to confirm the absence of the latter species in the western climate-only predicted range and to corroborate this assumption. Although the effects of habitat loss can be confused with climatic variables and/or can be more evident on different scales (Thuiller et al. 2004; Luoto et al. 2007; Reino et al. 2013), as may be the case of *H. lundii* and *I. langsdorffii*, we agree that the implementation of landscape variables in distribution models can help ecologists in understanding species distribution dynamics. True absence data is crucial for model validation. Nevertheless, gathering this data is difficult and time-consuming due to the wide phenological population fluctuations that anurans sometimes exhibit (Wells 2007). Moreover, higher rates of deforestation combined with the effects of the current climate change on species (Garcia et al. 2014) create a certain urgency for ecological studies to support solid conservation plans. Thus, modeling approaches that incorporate habitat landscape metrics, particularly for species dependent on the habitat integrity, can be a helpful tool for identifying areas where these species may have occurred before habitat loss took place and/or to assess how climate change can influence species distribution under several land use scenarios (Reino et al. 2013; Tian et al. 2014).

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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