

Invasive American bullfrogs and African Clawed Frogs in South America: High Suitability of Occurrence in Biodiversity Hotspots

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Fabiana G. Barbosa, Camila Both, and Miguel B. Araújo (2017) Invasion of protected areas by non-native species is currently one of the main threats to global biodiversity. Using an ensemble of bioclimatic envelope models we quantify the degree of exposure of South American protected areas to invasion by two invasive amphibian species. We focus on protected areas that coincide with global biodiversity hotspots. The species modeled, *Lithobates catesbeianus* and *Xenopus laevis*, have been reported to threaten local faunas in several non-native areas that they invaded, including areas in Asia, Europe, North America, and South America. We show that 87.5% of the protected areas within the Atlantic Forest may be most at risk of invasion by *L. catesbeianus* and *X. laevis* under current climate conditions, followed by areas in the Cerrado (51.7%), Tropical Andes (37.6%), Tumbes-Choco-Magdalena (22.5%), and Chilean Winter Rainfall and Valdivian Forests (20.5%). Conservation plans for these regions should, therefore, consider latent threats from multiple sources including invasion by highly competitive non-native species such as the ones modeled in our study.

Key words: Biological invasions, Bioclimatic envelope models, *Lithobates catesbeianus*, Protected areas, *Xenopus laevis*.

BACKGROUND

Protected areas (henceforth PAs) are one of the cornerstones of spatial conservation planning for biodiversity (Margules and Pressey 2000). While the total coverage of PAs has been increasing worldwide (Jenkins and Joppa 2009). PAs are facing increasing pressures such as unsustainable levels of tourism, financial shortfalls, poaching and other extractive activities, deforestation and habitat fragmentation, encroachment by urbanization and other human activities, and invasion by non-native invasive species (Ervin 2003).

Invasions by non-native amphibian species have been reported in several parts

of the world (Kraus 2009). In South America, two invasive amphibian species have received particular attention from researchers: *Lithobates catesbeianus* (Shaw 1802) and *Xenopus laevis* (Daudin 1802) (e.g., Lobos and Jaksic 2005; Laufer et al. 2008; Lobos et al. 2013). *Lithobates catesbeianus*, known as the American bullfrog, is native to eastern North America and its global distribution includes 41 countries (Ervin 2003; Frost 2013). In South America, *L. catesbeianus* is present in ten countries (Ervin 2003; Frost 2013) with populations established in a variety of environments (e.g., Laufer et al. 2008; Lobos et al. 2013; Ferreira and Lima 2012), including PAs (Lucas and Fortes 2008; Schüttler and Karez

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2008; Both et al. 2011; Madalozzo et al. 2016). Invasive populations of *L. catesbeianus* in new environments have caused substantial damage to native fauna through competition (e.g., Kupferberg 1997; Pearl et al. 2004), predation (e.g., Silva et al. 2011; Boelter et al. 2012), or acoustic interference (e.g., Both and Grant 2012). For these reasons, *L. catesbeianus* has been listed among the “100 worst invasive species” by the International Union for Conservation of Nature (IUCN) (Lowe et al. 2000). *Xenopus laevis*, known as the African clawed frog, is native to Mediterranean zone of the Cape Region of South Africa (see Lobos et al. 2013 for details), but has invaded extensive areas on several continents (see Measey et al. 2012 for review). In South America, *X. laevis* is present in natural and disturbed environments in Chile (Lobos and Jaksic 2005; Lobos et al. 2013), but to our knowledge there are no records in PAs. Damage documented for *X. laevis* includes consumption of native prey (Lafferty and Page 1997) and reducing reproductive rates of native amphibians (Lillo et al. 2011). *Lithobates catesbeianus* and *X. laevis* are both recognized as vectors of the fungus *Batrachochytrium dendrobatidis*, which is lethal to many other amphibians and has been linked with amphibian declines (e.g., Garner et al. 2006; Solis et al. 2010).

Eradication of *L. catesbeianus* and *X. laevis* is difficult once populations are established in non-native ranges (Fouquet and Measey 2006; Adams and Pearl 2007). Preventive action is therefore required to prevent or slow the rate of spread of these invasive species in PAs. Of particular interest is the identification of areas where both species are likely to invade, as these are areas where the effects of these two species could be additive.

In the last decades, bioclimatic envelope models (henceforth BEMs) have become one of the main tools for predicting the distribution of suitable climatic areas for the establishment of invasive species (Jiménez-Valverde et al. 2011; Barbosa et al. 2012). Such models are built using modelling methods that establish correlations between the geographic distribution of a species and a set of predictor variables (typically climatic) to identify conditions that are suitable for maintaining viable populations (see Araújo and Peterson 2012 for review on BEMs). Currently, multiple methods are now available for modelling bioclimatic (see Peterson et al. 2011 for review). Many studies have demonstrated that different methods calibrated using the same dataset can provide different predictions (e.g., Elith et al.

2006; Tsoar et al. 2007), raising the possibility that no single “best” method exists (Pearson et al. 2006). To handle such algorithmic uncertainties, Araújo and New (2007) advocate the fitting of ensembles of BEMs. In some instances, BEMs used to predict the distribution of suitable climatic areas of invasive species were fitted using data from the native range of the invasive species (e.g., Giovanelli et al. 2008), implicitly assuming that the present distribution of the species is at equilibrium with the current climate (Araújo and Pearson 2005). However, some models using data from the native ranges of invasive species have been able to accurately predict areas of introduction, but not necessarily the total area of invasion (e.g., Broennimann et al. 2007; Barbosa et al. 2013). This failure to predict the extent of invasions has been attributed to a low degree of equilibrium with climate in their native range (Peterson 2011). To reduce such biases in estimates of a species’ potential distribution it has been suggested that, whenever possible, data from the entire range (native and invaded) should be used when building models (Broennimann and Guisan 2008; Beaumont et al. 2009a).

In this context, we quantified the degree of exposure of South American PAs to invasion by *L. catesbeianus* and *X. laevis* under current climate conditions. We focused specifically on PAs that coincide with biodiversity hotspots in South America (Atlantic Forest, Tropical Andes, Chilean Winter Rainfall and Valdivian Forests, and Tumbes-Choco-Magdalena), as they are likely to be of greater importance for conservation. First, for each invasive species, we built an ensemble of BEMs using data from both its native and invaded ranges in order to estimate a broad range of climatically suitable areas for establishment of the species in South America. Second, we combined these predictions to build a map that shows the areas climatically suitable for the establishment of the two invasive species in South America. Third, we overlaid the PAs with the map of climatic suitability for the two invasive species modeled in order to assess the degree of exposure of PAs to invasion. Finally, we calculated the potential surface of each biodiversity hotspot in South America that may be most at risk of invasion by both species.

MATERIALS AND METHODS

Species data and bioclimatic variables

We obtained worldwide native and invasive presence records for *L. catesbeianus* and *X. laevis* from the Global Biodiversity Information Facility online database (GBIF; <http://data.gbif.org>) and from other published sources (see Supplementary 1). A total of 2,140 presence records were compiled for *L. catesbeianus*, 1,263 from within its native range (eastern North America) and 877 from invaded areas in Asia, Europe, western North America, Central America and South America. For *X. laevis*, 175 records were obtained, 93 from its native range (Mediterranean zone of the Cape Region of South Africa) and 82 from invaded areas in Asia, Europe, North America, and South America.

We extracted 19 current bioclimatic variables from the WorldClim database (Hijmans et al. 2005; see <http://www.worldclim.org> for description of the variables) with a spatial resolution of 10 arc-minutes. We then selected six bioclimatic variables: (i) mean temperature diurnal range (mean of the monthly difference of the maximum and minimum temperatures), (ii) temperature seasonality, (iii) mean temperature of wettest quarter, (iv) annual precipitation, (v) precipitation of driest month, and (vi) precipitation seasonality. These bioclimatic variables were selected based on the basis of studies carried with the two invasive species (Nori et al. 2011a; Loyola et al. 2012, Lobos et al. 2013), excluding highly correlated variables (pair-wise $r_{\text{Pearson}} < 0.75$; Braunish et al. 2013) to reduce multicollinearity and subsequent model over-fitting (Jiménez-Valverde et al. 2011).

We built two equal-area grids (0.16×0.16 degrees of latitude/longitude). The first grid covered the study area for *L. catesbeianus* (the full extent of its native range in eastern North America and in invaded areas), and the second covered the study area for *X. laevis* (in its native range in Mediterranean zone of the Cape Region of South Africa as well as in invaded areas). We then mapped all the presence records of each species into its study area to generate a grid cell matrix. We also resampled the values of each bioclimatic variable in each grid cell. The grids were generated using the software Spatial Analysis in Macroecology (SAM v.4.0; Rangel et al. 2010). All analyses below were performed using the data obtained from these grid cell matrices.

Bioclimatic envelope modelling

For each species, we built an ensemble of the BEM (Araújo and New 2007) using four presence-only methods. Models were fitted using the BIOENSEMBLES software for computer-intensive modelling of species potential distributions (Diniz-Filho et al. 2009). BIOENSEMBLES, user-friendly software, is an integrated framework for ensemble forecasting of species distributions that has modeling methods with different strategies of adjustment and type of input data (Terribile et al. 2012), such as presence-absence records methods (e.g., Generalized Linear Model), presence-background methods (e.g., Maxent), presence-pseudoabsence methods (e.g., GARP), and presence-only methods (e.g., BIOCLIM) (Peterson et al. 2011). Herein, the methods used were BIOCLIM (e.g., Busby 1991), Euclidean Distance (e.g., Farber and Kadmon 2003), Gower Distance (e.g., Carpenter et al. 1993), and Mahalanobis Distance (e.g., Farber and Kadmon 2003). Presence-only methods were chosen because absence records do not always imply a lack of climatic suitability (see Bradley 2009 for more details).

We obtained BEMs as follows. First, for each method, BEMs were built using a calibration subset of 70% of all the presence records (i.e., native and invasive range) selected at random and then evaluated with the remaining 30%; this process was repeated 50 times. We use 63 possible combinations ($2^n - 1$, where “n” is the number of variables) of the six bioclimatic variables (Diniz-Filho et al. 2009; Collevatti et al. 2013). Thus, for each species and modeling method used, our modeling procedure yielded 3150 BEMs (63 combinations of bioclimatic variables \times 50 cross-validation). Then continuous predictions of the models were converted into a binary vector of 0/1, indicating forecasted presences and absences in each grid cell using a cut-off point. True Skill Statistics (TSS) (Allouche et al. 2006), varying between -1 and 1, was used to evaluate the performance of the models. Finally, all models outputs with TSS > 0.5 were combined (an average weighted by the TSS value of each model) to generate a map of the frequency of BEM supporting the occurrence of species in each grid cell (Diniz-Filho et al. 2009; Collevatti et al. 2013). Herein we use these frequencies of occurrence of a species as a proxy of climatic suitability for the establishment of the invasive species in each grid cell.

We then built a map of climatic suitability for each species using the outputs of the BEMs, interpreted as an index of the potential for establishment for the species in South America. We then overlaid the maps of species to obtain a combined estimate of the potential for establishment of the two invasive species in South America. All maps were built using the software ArcGIS 10 (ESRI 2010).

Protected areas

We identified PAs in South America that may be most at risk of invasion by *L. catesbeianus* and *X. laevis* under current climate conditions, focusing on PAs that coincide with global biodiversity hotspots. Firstly, we downloaded the polygons of the biodiversity hotspots in South America from Conservation International (<http://www.conservation.org/>) as well as the polygons of the PAs from the World Database on Protected Areas (<http://www.protectedplanet.net/>). Second, we filtered the PAs to retain only those PAs that overlapped with biodiversity hotspots in South America. This resulted in 593 PAs within biodiversity hotspots in South America. Finally, we overlaid the PAs within biodiversity hotspots that coincided with the map of modeled climatic suitability for the two invasive species in order to assess the degree of exposure of PAs to risk of invasion. In addition, we also calculated the potential surface of each biodiversity hotspot in South America that may be most at risk of invasion by both species.

All spatial analyses were performed using the software ArcGIS 10. We only considered strict PAs (PA categories I – IV, International Union for Conservation of Nature (IUCN)) (UNEP-WCMC

2012). We used five classes of risk of invasion according to the climatic suitability of the total area in the PA (0 to 20, 20 to 40, 40 to 60, 60 to 80, and 80 to 100%), which we designate as presenting no, low, medium, high, and critical invasion risk, respectively.

RESULTS

Current climatically suitable areas coincided strongly with areas in which the invasive species have already been recorded in South America (Fig. 1a and 1b). Furthermore, low climatic suitability for *L. catesbeianus* was predicted in central eastern parts of Brazil, southeastern and northwestern portions of Argentina, northern Chile, southwestern Bolivia, the coast of Peru, the eastern portion of Colombia, and the southern and northern portions of Venezuela (Fig. 1a). For *X. laevis*, low climatic suitability was predicted in major portions of the northern and central eastern parts of the continent, southwest Bolivia, a southern portion of Peru, the northern and southern portions of Chile, and the northwest, southern and central western portions of Argentina (Fig. 1b). In parallel the combination of the current climatically suitable areas of both species (Fig. 1a and 1b) showed a large overlap in the potential distribution of *L. catesbeianus* and *X. laevis* in South America (Fig. 1c).

According to the models, up to 87.5% of the PAs within the Atlantic Forest may be at risk of invasion by *L. catesbeianus* and *X. laevis* under current climate conditions, followed by the Cerrado (51.7%), Tropical Andes (37.6%), Tumbes-Choco-Magdalena (22.4%), and Chilean Winter Rainfall and Valdivian Forests (20.5%) (Table 1). Additionally, 74.72% of the surface of the Atlantic

Table 1. Percentage of Protected Areas suitable (*i.e.*, Percentage by number of Protected Areas suitable) within each biodiversity hotspot in South America that may be most at each class of risk from invasions of both non-native invasive species (*Lithobates catesbeianus* and *Xenopus laevis*) under current climate conditions

Biodiversity hotspot	Class of risk				
	Critically 1 - 0.8	High 0.8 - 0.6	Medium 0.6 - 0.4	Low 0.4 - 0.2	None 0.2 - 0
Atlantic Forest	87.5	0.0	0.0	0.0	12.5
Cerrado	51.7	0.0	2.5	0.0	45.8
Chilean Winter Rainfall and Valdivian Forests	20.5	0.0	2.6	10.2	66.7
Tropical Andes	37.6	1.5	3.8	0.7	30.8
Tumbes-Choco-Magdalena	22.5	0.0	2.8	15.4	59.3

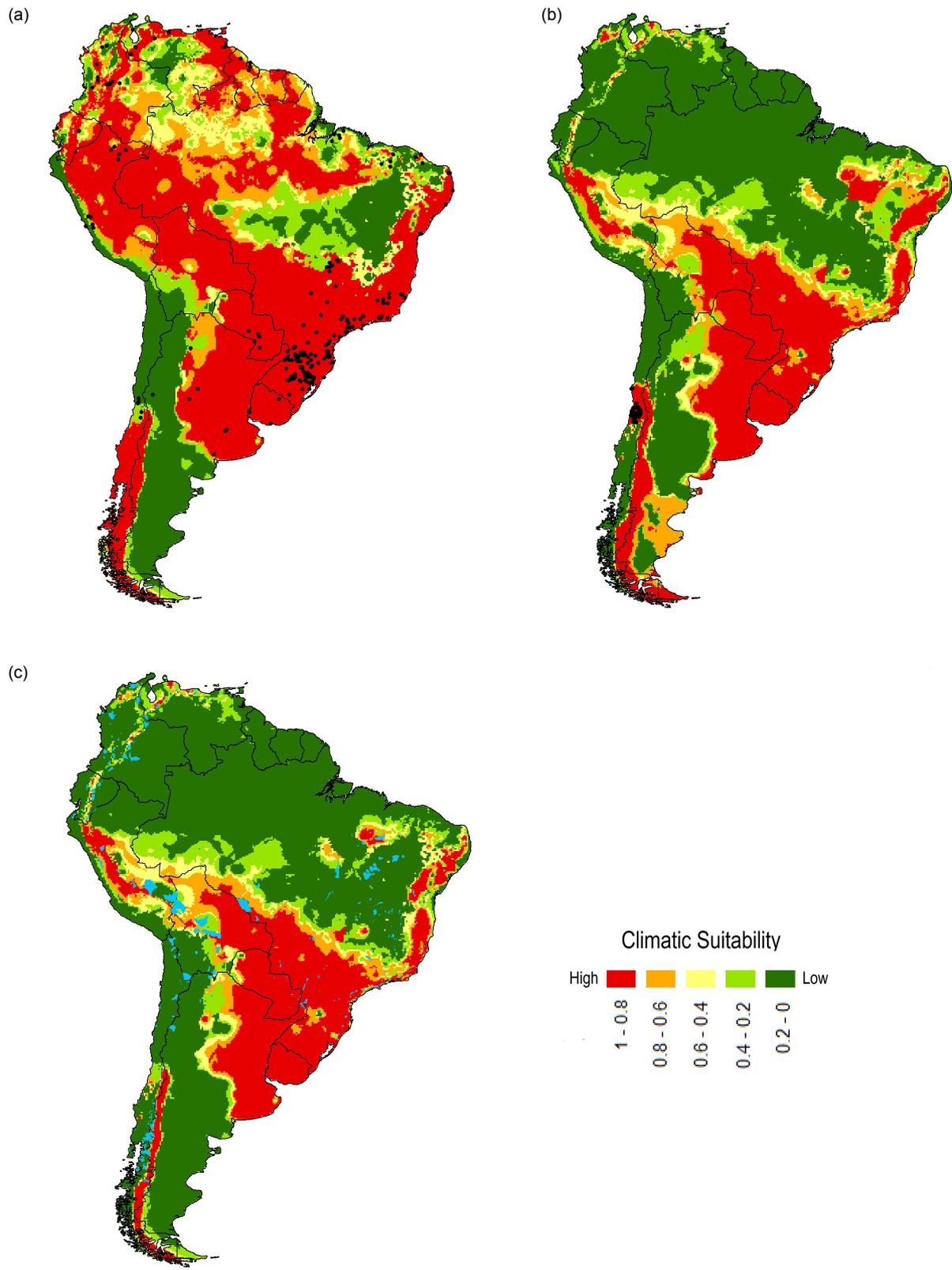


Fig. 1. Map of climatic suitability for the establishment of *Lithobates catesbeianus* (a), *Xenopus laevis* (b), and of both species (c) in South America. Black dots indicate presence records of the species and blue are Protected Areas within biodiversity hotspots in South America.

Forest was projected as a suitable climatic area for the establishment of both non-native invasive amphibian species, followed by the Cerrado (28.04%), Tropical Andes (21.23%), Chilean Winter Rainfall and Valdivian Forests (15.15%), and Tumbes-Choco-Magdalena (1.64%) (Fig. 2).

DISCUSSION

Prediction in the early stages, with subsequent prevention, is the most effective management strategy for invasive species, and is often the most efficient too (Richardson and Thuiller 2007). Bioclimatic envelope models are one potentially useful tool to predict climatically suitable areas for the establishment of invasive species in non-native areas (Jiménez-Valverde et al. 2011), as well as in PAs (e.g., Beaumont et al. 2009b; Vicente et al. 2013). For instance, in the case of *L. catesbeianus*, two studies modeled the potential distribution of the species in PAs in South America. Nori et al. (2011b) modeled the potential distribution of *L. catesbeianus* in PAs (six IUCN categories) in South America, concluding that over 30% of the surface of all the IUCN PAs in South America are climatically suitable for establishment of the species under current conditions. On the other hand, Loyola et al. (2012) modeled the potential distribution of *L. catesbeianus* in PAs

(IUCN categories I - IV with PAs > 5000 hectares) in the Brazilian Atlantic Forest and showed that several PAs are suitable for establishment of the species under current conditions. In contrast, to our knowledge no studies have quantified the degree of exposure of PAs to invasion by *X. laevis* in South America using BEMs. Here, we quantified, for the first time, the percentage of suitable PAs within each biodiversity hotspot in South America that may be most at risk of invasion by *L. catesbeianus* and *X. laevis* (Fig. 2a) under current climate conditions. Our results show that several PAs within biodiversity hotspots in South America may be at risk of invasion by *L. catesbeianus* and *X. laevis* under current climate conditions (Table 1). Although there were differences in the percentage of suitable PAs among biodiversity hotspots, our results indicate that all biodiversity hotspots in South America have PAs that may be at risk of invasion by both species (Fig. 2) (also see Supplementary - figure A1, which provides results for each invasive species).

The biodiversity of amphibian species peaks in tropical regions, especially in biodiversity hotspots in South America (Myers et al. 2000), making this a critical region for amphibian conservation. However, a large amount of the native habitat in biodiversity hotspots in South America has been transformed into numerous smaller isolated patches (e.g., Silva and Bates 2002; Armenteras et al. 2003; Ribeiro et al. 2009; Sarkar et al. 2009) and, consequently, many current PAs are increasingly isolated, especially PAs within the Atlantic Forest and the Cerrado (e.g., Silva and Bates 2002; Ribeiro et al. 2009), which in turn make the PAs more susceptible to invasion. Additionally, amphibians are thought to be the most threatened vertebrate group and many authors consider that they are declining globally (e.g., Stuart et al. 2004). Invasive species have been suggested as a possible extrinsic cause of amphibian decline (Kats and Ferrer 2003) together with climate change, changes in land use and disease (Hof et al. 2011). In invaded areas, *L. catesbeianus* and *X. laevis* have caused substantial ecological damage to native organisms, especially to native species of amphibian (e.g., Kraus 2009; Lillo et al. 2011). In the case of *L. catesbeianus*, the decline of some native amphibian species has been associated with its establishment worldwide (e.g., Kupferberg 1997); but see also Pearl et al. 2004 and Kats and Ferrer 2003), although evidence that the species is negatively affecting local amphibian

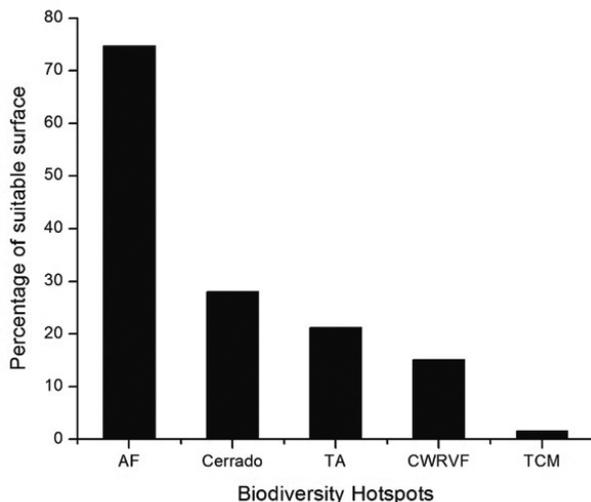


Fig. 2. Percentage of suitable surface within each biodiversity hotspot in South America that may be most at risk from invasions of both non-native invasive species (*Lithobates catesbeianus* and *Xenopus laevis*) under current climate conditions. AF = Atlantic Forest, TA = Tropical Andes, CWRVF = Chilean Winter Rainfall and Valdivian Forests, TCM = Tumbes-Choco-Magdalena.

communities in South America is still lacking (Both et al. 2014). In addition, *L. catesbeianus* and *X. laevis* are recognized as vectors of the fungus *Batrachochytrium dendrobatidis* (e.g., Solis et al. 2010; Schloegel et al. 2010), the agent responsible for chytridiomycosis, a disease considered one of the main causes of decline and extinction in amphibian populations worldwide (Daszak et al. 2003; Skerratt et al. 2007). Therefore, the presence of *L. catesbeianus* and *X. laevis* in South American PAs is dangerous.

A range of preventive measures for *L. catesbeianus* and *X. laevis* in South America has been recommended in previous studies (Giovanelli et al. 2008; Nori et al. 2011a, b; Urbina-Cardona et al. 2011; Loyola et al. 2012; Lobos et al. 2013). We agree with these studies and reinforce the urgency in implementing effective prevention programs in South American PAs. Another issue to consider is that *L. catesbeianus* and *X. laevis* have already established populations in some South American hotspots (Both et al. 2011; Sanabria et al. 2011), including PAs in the case of *L. catesbeianus* (Lucas and Fortes 2008; Schüttler and Karez 2008; Both et al. 2011). Populations of *L. catesbeianus* and *X. laevis* are difficult to eradicate once established (Fouquet and Measey 2006; Adams and Pearl 2007) and, according to Leung et al. (2002), eradication programs are less cost-effective than prevention programs. However, several methods have been proposed to eradicate and/or control *L. catesbeianus* in North America (see Louette et al. 2012 for some proposed methods). Additionally, for both invasive species, authors have recommended interventions to reduce the permanency of lentic systems, as an eradication and/or control measure (e.g., Fuller et al. 2011; Lobos et al. 2013; Peterson et al. 2013). Water permanency is an environmental gradient well known to structure lentic communities (see Wellborn et al. 1996). Thus, such measures should be carefully and particularly considered, since they can have more negative impacts upon native fauna than the invasive species itself. Therefore, in parallel with prevention programs, we also recommend strict control of activities that represent high-risk pathways for accidental and/or intentional introduction of these species in natural environments (e.g., frog farms and the pet trade).

CONCLUSIONS

In summary, our study is the first to quantify the degree of exposure of South American PAs to invasion by *L. catesbeianus* and *X. laevis*, and such information provides a valuable baseline for implementing management programs. Moreover, our results showed a large overlap in the potential distribution of *L. catesbeianus* and *X. laevis* in South America (Fig. 1c). Therefore, we suggest that future studies should assess the potential impact of co-occurrence of these invasive species upon native fauna (e.g., Araújo et al. 2011). Knowledge about the effects of interactions among competing species could provide additional support to decision making on eradication and/or control and prevention priorities.

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Supplementary 1. Sources of presence records for *L. catesbeianus* and *X. laevis*. (download)

Supplementary - Fig. A1. Percentage of suitable surface within each biodiversity hotspots in South America that may be most at risk from invasions of *Lithobates catesbeianus* and *Xenopus laevis* under current climate conditions. AF = Atlantic Forest, TA = Tropical Andes, CWRVF = Chilean Winter Rainfall and Valdivian Forests, TCM = Tumbes-Choco-Magdalena. (download)