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Aliens in the backyard: Did the American bullfrog conquer the habitat of native frogs in the semi-deciduous Atlantic Forest?

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The American bullfrog *Lithobates catesbeianus* has a natural distribution in North America, but was spread by human activities in different regions around the world. It is listed as the most invasive amphibian species, affecting terrestrial and aquatic ecosystems and the community of native species. In addition, the American bullfrog is extensively associated with lethal pathogens, with high correlation of the presence of this species with population declines and extinctions. Here we test if this alien species has spread through the landscape, establishing populations at new locations. We used diverse methods including georeferencing of satellite images, ethnobiological interviews and field data to evaluate the dispersion and effects of *L. catesbeianus* introduction on amphibian composition, species number, and density of individuals in forest fragments in an Atlantic Forest landscape. We did not find any relationship between density of individuals, number of species or composition of the native anuran assemblages in forest fragments in relation to the presence or proximity of American bullfrog introduction points. Additionally, we found that the dispersion potential of this species in the studied landscape is zero, as it was only found in those fragments where it was specifically introduced 15 years ago. The species has not established new populations in the landscape. Although exotic, *L. catesbeianus* thrives in lentic habitats and has no apparent effect on the structural metrics of the native anuran assemblage. Despite this alien species exhibiting a capacity to adapt and survive at the point of introduction, its potential for propagation is limited probably by the fragmented terrestrial landscape and regional stream network.

Keywords: amphibians; anurans; biological invasions; community ecology; exotic species; fragmented landscape; freshwater biology; landscape ecology.

INTRODUCTION

The American bullfrog, *Lithobates catesbeianus* (Shaw, 1802), has a natural distribution that runs from northern Mexico to southern Canada, but with foci of introduction in different regions around the world (IUCN, 2019), indicating the species' adaptability in different latitudes and biomes. In Brazil, most introduction points are located in the Atlantic Forest biome (Both et al., 2011). Studies for the Atlantic Forest report that *L. catesbeianus* may compete acoustically with native species (Both & Grant, 2012), and prey upon a variety of species ranging from invertebrates to vertebrates, including many native amphibian species from different families (Silva et al., 2011; Boelter et al., 2012; Silva et al., 2016). In addition, bullfrogs were reported to be a reservoir of spores that transmit pathogens such as the fungus *Batrachochytrium dendrobatidis* (*Bd*), which is lethal to anurans (Schloegel et al., 2010; Schloegel et al., 2012; O' Hanlon et al., 2018), especially in highly anthropised biomes, such as the Atlantic Forest.

The Atlantic Rainforest is severely fragmented and has less than of 11 % of its original extent, including the small forest fragments (Ribeiro et al., 2009). It harbours many endemic and non-endemic amphibian species, representing 7.7 % of amphibian species in the world (Rossa-Feres et al., 2017). Several declines in amphibian populations have been reported for the Atlantic Rainforest (Heyer et al., 1988, Weygoldt et al., 1989; Eterovick et al., 2005). However, the causes of many of these declines are not well understood (Stuart et al., 2004). Recently, studies showed that the fragmentation, disconnection of terrestrial and aquatic habitats, agricultural crops, livestock and the degradation of vegetation quality in the forest remnants have been associated with local extinctions of anurans in the Atlantic Rainforest (Becker et al., 2007; Ferrante et al., 2017). However, there are few studies about the possible impact of *L. catesbeianus* on native amphibian assemblages in the Atlantic Forest (Both et al., 2014). Considering the critical conservation situation of the biome and the wide distribution of this species, it is important to understand the dispersal capacity and the potential impact of this exotic species on the native anurans.

It is known that the landscape configuration, such as the arrangement of the fragments and the surrounding

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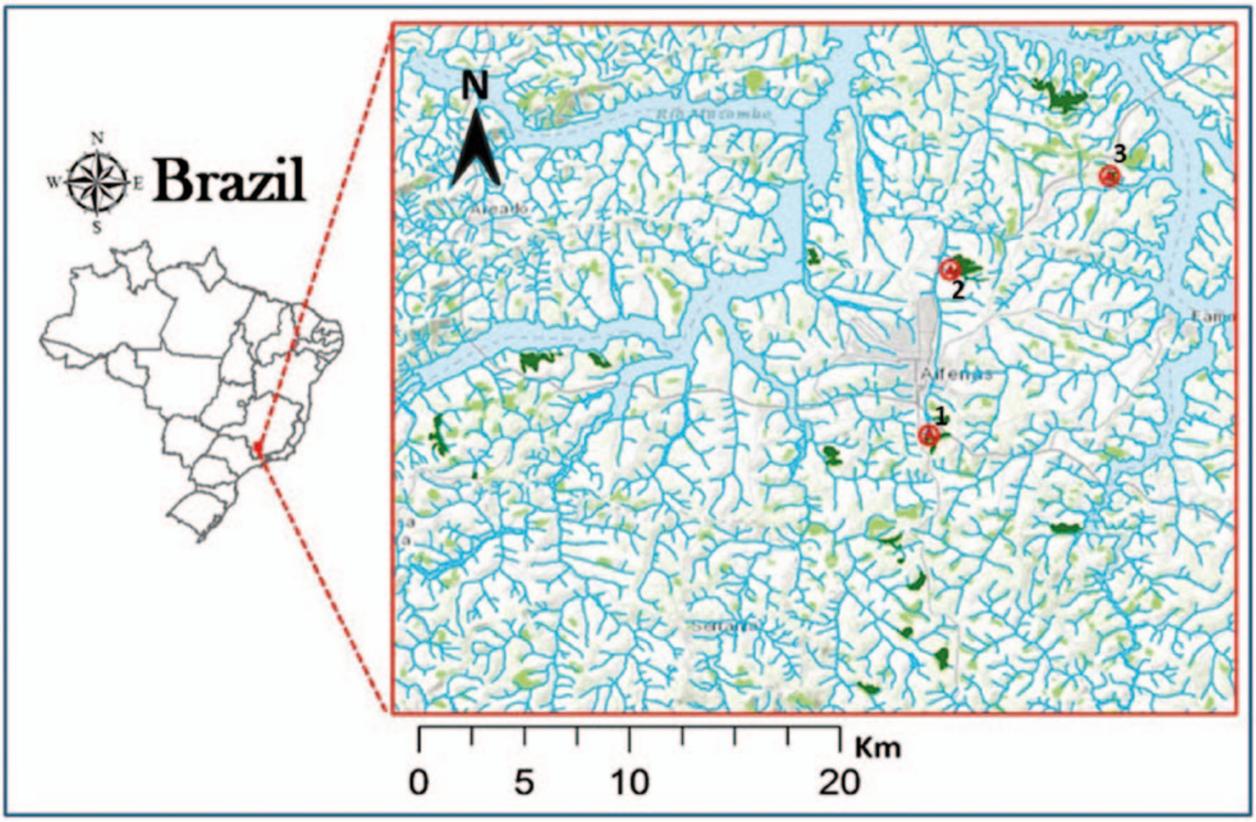

Figure 1. Studied landscape in Minas Gerais state, Brazil. The three introduction points of the exotic species *L. catesbeianus* are represented by circled red triangles, the forest fragments sampled are highlighted in dark green, and the other forest fragments present in the landscape are in light green. The stream network is highlighted in blue.

matrices affect anuran assemblages (Ferrante et al., 2017). The landscape configuration in protected areas, such as the forest-edge-agriculture gradient could facilitate the dispersal of *L. catesbeianus* (Madalozzo et al., 2016). However, little is known about how severely fragmented landscapes might affect the introduced *L. catesbeianus*. In this study, we evaluated 18 forest fragments surrounding three introduction points of the exotic *L. catesbeianus*, in order to test if the alien species has spread through the landscape, so establishing populations at new locations. We also tested the impact of *L. catesbeianus* on native anurans by relating the number of species, density and composition of the native anuran assemblages in these forest fragments with the distance from the *L. catesbeianus* introduction points.

MATERIALS AND METHODS

Study Site

The landscape investigated in this study was in the south of Minas Gerais state, Brazil (21°25038.42″ S; 45°56053.21″ W, Fig. 1.). The region has annual mean precipitation of 1,554 mm (Roldão et al., 2012), and is a typical agricultural area converted from original semi-decidual Atlantic Forest, with predominance of sun coffee, sugarcane and cattle pasture.

Sampling Design

We mapped the current *L. catesbeianus* occurrence points in the landscape and the time and process of introduction of this species by means of personal communications with rural workers and land owners. We sampled 18 forest fragments around three known points of bullfrog introduction. The anuran assemblages were sampled within each forest fragment by visual encounter surveys and playbacks of advertisement calls of local species. Each fragment was sampled simultaneously by three researchers along 300-m long and 20-m wide transects parallel to water bodies. Both post-metamorphic juvenile and adult individuals were considered in the sample. All forest fragments were sampled in three nocturnal occasions. The surveys were conducted between December 2011 and March 2012, comprising the local rainy season (Roldão et al., 2012) and the main amphibian breeding season in the Atlantic Forest (Haddad et al., 2013).

Statistical analyses

We compared the number of species between forest fragments with presence of bullfrog, or with bullfrogs at its periphery, and forest fragments with total absence of bullfrogs through rarefaction. We standardised our dataset by the number of individuals, which accounts for sample heterogeneity maintaining the intrinsic abundance relationships between species (Gotelli & Colwell, 2001). We used an analytical method to generate valid confidence intervals (CIs) for the rarefaction curves, which do not converge to zero at the maximum sample size (Colwell & Elsensohn, 2014). We also used analysis of variance (ANOVA) to compare the number of species and abundance of native species between forest fragments with presence and absence of bullfrogs.

We also used ArcGIS 10 software to measure the shortest linear distance between the points of introduction of the alien species and the distance to each forest fragment surveyed. We used the shapefile of Atlantic forest fragments (SOS Mata Atlântica) and the stream network of the Brazilian ANA (Agência Nacional de Águas). We then, through simple linear regression, related the number of native species and the density of individuals in the forest fragments to the distance in a straight line between the nearest point of *L. catesbeianus* introduction for each fragment. We also used permutational multivariate analysis of variance (PERMANOVA), based on the Bray-Curtis similarity index for abundance and Sorensen data for presence and absence data, to investigate the relationship between the composition of native species and the distance in a straight line between the entry point of *L. catesbeianus* closest to each fragment. The significance values obtained in the analyses were based on 999 permutations. All analyses were performed in the R (R Core Team, 2017) computational environment with the vegan community ecology package (Oksanen et al., 2018).

RESULTS

Local farmers reported that human-caused introductions occurred in three locations at least 15 years ago (Fig. 1). Via interviews with landowners and rural workers in the proprieties, we received three different explanations for the introduction of the exotic species in the regional landscape: 1 - fugitives, where some individuals escaped from breeding ranches to the environment and established a breeding population in a pond adjacent to the ranch (less than 100 meters); 2 - intentional introduction in an artificial lake at the edges of a forest fragment for consumption; 3 - liberation of individuals with the mistaken intention of promoting local biodiversity. Three populations were observed in artificial ponds, with no water flow, at the edge of forest fragments. Although all the artificial lakes housing *L. catesbeianus* had connections to natural waterbodies running into adjacent forest fragments, bullfrogs were only observed in the fragment corresponding to introduction point 3 (Fig. 1), although the other two bodies of water with the presence of the exotic species were in contact with forest fragments.

In the 18 sampled forest fragments, we found 18 native species of anurans belonging to six families: Bufonidae, Craugastoridae, Hylidae, Leptodactylidae, Odontophrynidae and Phyllomedusidae. The number of anuran species varied from 1 to 7 between forest fragments, and two forest fragments harboured no anuran species. Although depauperate, the accumulation curves were similar between fragments with and without *L. castesbeianus* (Fig. 2). Both the number of species (ANOVA: $F_{1,16}$ = 0.315, p = 0.582, Fig. 3A) and density of individuals (ANOVA: $F_{1,16}$ = 0.014, p = 0.906, Fig. 3B) were similar between forest fragments with and without *L. catesbeianus*. We found no relationship between either the distance from the American bullfrog

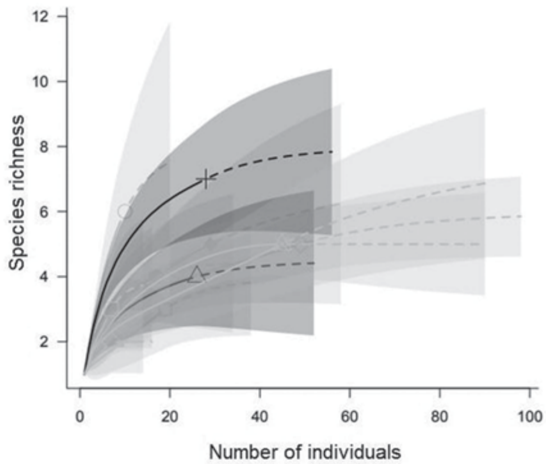

Figure 2. Species rarefaction curves (solid lines) in the invaded (black) and non-invaded (grey) fragments by the bullfrog in Minas Gerais state, Brazil. Dotted lines indicate number of species extrapolation. Shaded grey area represents the 95 % confidence intervals.

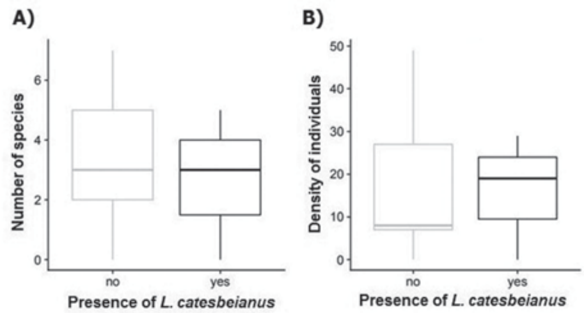

Figure 3. Number of species **(A)** and density of individuals **(B)** in the three invaded (black) and 15 non-invaded (grey) fragments by the bullfrog in Minas Gerais state, Brazil.

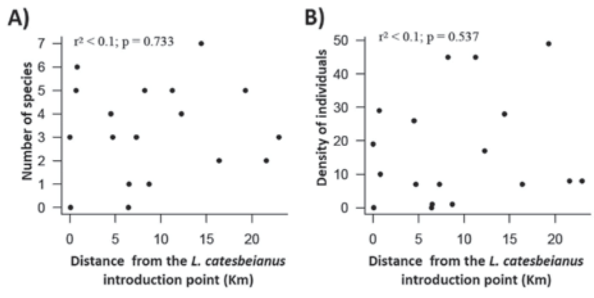

Figure 4. Relationship between the distance to the introduction point of *L. catesbeianus* and metrics related to the native anuran assemblages for each forest fragment.

introduction points and the number of species (r^2 <0.1, p = 0.733, Fig. 4A) or density of individuals (r^2 <0.1, p = 0.537, Fig. 4B) in the native anuran assemblages of the sampled forest fragments. Based on presence/absence data, NMDS analysis also failed to detect an impact on either structure of the native anuran assemblages within the forest fragments (PERMANOVA: R^2 = 0.07, p = 0.314, Fig. 5A), or population density data (PERMANOVA: R^2 = 0.08, p = 0.296, Fig. 5B) in relation to the distance from the introduction points of this exotic species. Inside the forest fragment with occurrence of *L. catesbeianus*, an individual of this species lacking a hind limb was captured. At the same site, a second individual bearing the same morphological anomaly was seen but not collected.

DISCUSSION

The results of ecological modelling conducted by Giovanelli et al. (2008) and Forti et al. (2017) are the closest to our field-based findings. Although Giovanelli et al. (2008) did not include the introduction points of *L. catesbeianus* in the landscapes we studied, modelling does not suggest the invasion of *L. catesbeianus* to the southern region of the state of Minas Gerais, where the predominant biome is a highly fragmented semi-deciduous Atlantic Forest. Therefore, distribution models based only on the environmental affinities of the species and which ignore whether the species in question has the dispersal capacity to overcome the natural or anthropic geographic barriers present in the studied region should the interpreted with caution (e.g., Loyola et al., 2012). Our results showed that the bullfrog was found only in the areas into which it was originally introduced, and had not dispersed to closely adjacent fragments, even when they were downstream. Thus, in the study region, as well as for most of the semi-deciduous Atlantic Forest, bullfrogs appear to have a null dispersion potential either by aquatic route (due to the water current) or by terrestrial route (due to the impermeability of the anthropic matrix).

However, we recommend that additional landscapes with invasive Bullfrog populations older than 15 years of introduction should also be studied to access the real dispersal potential of this alien species. We do not rule out that some bullfrog individuals may have dispersed into the landscape in the past, however our results point to a failure to establish new populations.

Forest fragmentation has been shown to be a barrier to forest-dependent anurans, causing inbreeding and genetic erosion in anuran populations in forest fragments in the Atlantic Forest (Dixo et al., 2009). The presence of morphological anomalies reported in this study coincides with the pattern observed in populations of amphibians with strong degrees of inbreeding (Bessa-Silva et al., 2016), which may be indicative of the low genetic diversity of the studied populations. The interpretation of low genetic diversity in *L. catesbeianus* is speculative, as there are no genetic studies on this topic at the current study site. However, the small number of individuals introduced into the sites associated with the strong commercial selection of the breeding individuals suggests inbreeding. Future studies should evaluate the genetic diversity of populations of this exotic species and their possible natural decline induced by genetic factors. Our results suggest that even years after the introduction of the bullfrog, the number of species in forest fragments with and without the bullfrog are similar. We also did not observe a reduction in the density of adult anurans at the sites where the American bullfrog was introduced. Our results echo other studies from southern Brazil where the presence of the invasive *L. catesbeianus* in ponds also did not change the composition of native amphibian assemblages (Both & Melo, 2015). In aquatic vertebrate communities invaded by the American bullfrog in Uruguay, rarefaction curves indicated no changes in species richness patterns (Gobel et al., 2018). However, Gobel et al., (2018) observed that the abundance of tadpoles for some species was significantly lower, although this was not universally the case for the tadpole stages of all species in the sampled anuran assemblage (Gobel et al., 2018). For the Atlantic Forest, the habitat fragmentation

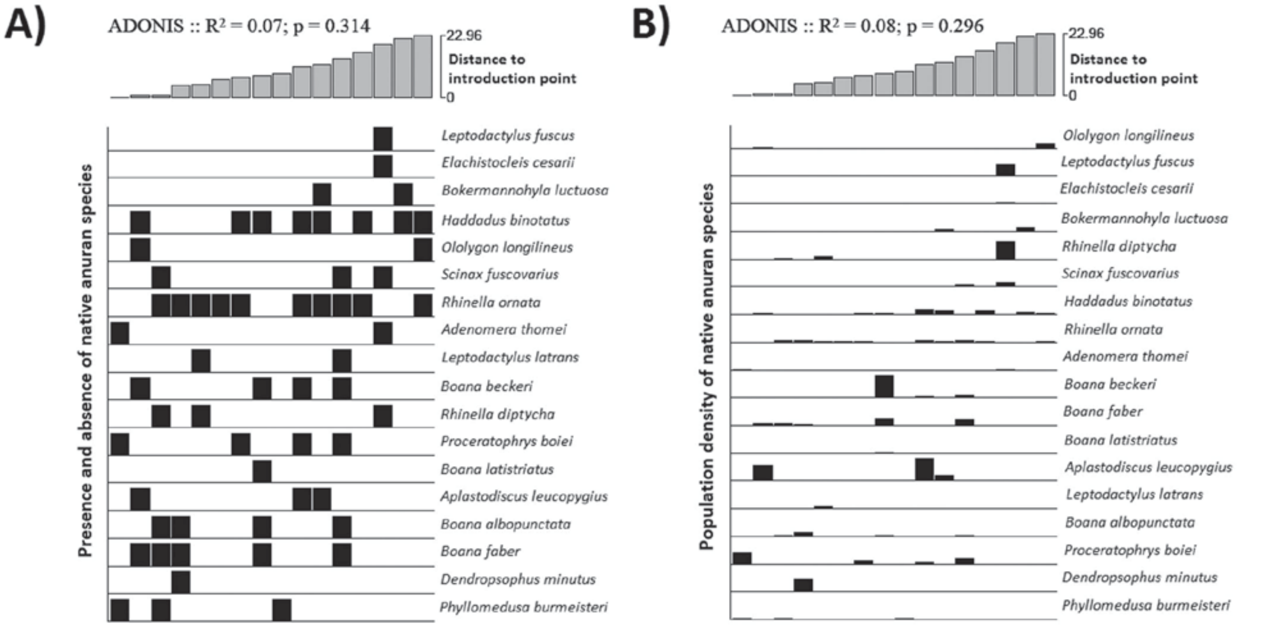

Figure 5. Composition of the native anuran assemblage in relation to distance to introduction point of *L. catesbeianus*. **(A)** Presence/absence of native species and **(B)** density of individuals.

and agricultural crops such as sugarcane and pastures for the livestock (Ferrante et al., 2017) seem to constitute a stronger threat to anuran assemblages by affecting density of individuals as well as richness and composition of species than does *L. castesbeianus* introduction.

In the studied landscape, species such as *Leptodactylus latrans* and *Leptodactylus labyrinthicus* occur (Ferrante et al., 2015). These species can be considered ecologically similar to American bullfrogs because of their equivalent body size, habitat use and reproductive mode (Kaefer et al., 2007, Haddad et al., 2013). The introduction of *L. catesbeianus* in a Cerrado (Brazilian Savanna) landscape has been reported to extirpate *L. latrans* and *L. labyrinthicus* (Batista, 2002). However, *L. latrans* and *L. catesbeianus* do not overlap in their food niche (Silva et al., 2016). *Leptodactylus labyrinthicus* naturally does not occur inside forests (Haddad et al., 2013), it was not found in any of the forest fragments, and no structuring of *L. latrans* presence or density was observed with greater proximity to *L. catesbeianus* introduction points (Fig. 5ab). The fact that *L. latrans* and *L. labyrinthicus* have habitat preferences for open areas (Haddad et al., 2013) may explain the absence of these species in the forest fragments without signifying any decline that can be associated with the presence of the American bullfrog in the landscape.

Even though studies report heavy predation by *L. catesbeianus* on native frogs (Silva et al., 2011, Boelter et al., 2012), it is not known to what extent predation by this exotic species affects recruitment or alters the density of native anuran species populations. In the landscape studied here, our data suggests that the amphibian density was not affected by the presence of the American bullfrog. In addition, juvenile bullfrogs are also reported to be eaten by native anuran species (Silva & Ribeiro-Filho, 2009), indicating that the species now forms part of the food web in the Atlantic Forest, and may therefore be under density-dependent regulation. Accordingly, our results add a new layer of complexity to studies of the introduction of the bullfrog in Brazil, demonstrating both a surprisingly imperceptible effect of this exotic species on the native assemblages at a landscape level.

The exotic species *L. catesbeianus* has been proposed as a reservoir of the *Bd* fungus (Schloegel et al., 2010), as well as being responsible for introducing an Asian *Bd* lineage in Brazil (O' Hanlon et al., 2018). However, in the current study, we found no evidence of native species declines or density reduction of amphibians in relation to the presence and distance of American bullfrog introduction foci, which is contrary to what would be expected if bullfrogs were either dispersing or harbouring some lethal pathogen.

CONCLUSIONS

Although *L. catesbeianus* is considered to be a generalist species due to its ability to survive in disturbed environments (IUCN, 2019), this species tends to establish populations in lentic water bodies (Boelter et al., 2012, Haddad et al., 2013, IUCN, 2019). As a result, the local waterbody network may also act as a natural barrier in the study landscape, since it is composed mostly of flowing streams. In addition, severe landscape fragmentation and agricultural crops may further limit bullfrog dispersal capacity through land. Our results suggest that, although exotic, *L. catesbeianus* is not invasive at the landscape level and does not exert a negative impact on native anuran assemblages in the severely fragmented landscapes of the Atlantic Forest investigated by this study.

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