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Introduction pathways and socio-economic variables drive the distribution of alien amphibians and reptiles in a megadiverse country

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Abstract

Aims: We identify alien reptiles and amphibians, invaders or not, in Brazil and evaluate the following: (a) which alien species are found in the country; (b) where they originate from; (c) how they are distributed; (d) why and how they were introduced; and (e) which factors affect the record incidences and local richness of these species.

Location: Brazil.

Methods: We conduct a comprehensive survey of different data sources to collect records of alien amphibians and reptiles. We then use a causal model approach to evaluate the influence of space, climate, anthropogenic predictors, and introduction pathways on alien richness and number of records.

Results: We find a total of 2,292 records of 136 species of alien reptiles and amphibians. Although species from many regions of the world can be found, most are snakes, lizards and anurans originating in the Americas. Although records of alien amphibians and reptiles are found throughout Brazil, they are concentrated in more economically developed areas. Socio-economic measures have both a direct and indirect causal relationship over the distribution of alien species and affect all introduction pathways, which are key factors explaining the alien species' distribution. Pet trade was directly related to alien diversity, while all the three introduction pathways contributed to explain the number of records.

Main Conclusions: We reveal a high diversity of alien amphibians and reptiles widespread in an already megadiverse country. The finding that alien richness occurs in highly populated and wealthy areas and that it is linked to the pet trade helps to direct efforts towards the surveillance and prevention of the spread of alien species in Brazil. A higher record incidence is associated with species introduced accidentally or for human consumption, mainly represented by a few already invasive widespread species, impairing management measures.

KEYWORDS
alien, Brazil, human activity, invasive, pet trade

1 | INTRODUCTION

Invasive species can cause ecological, economic and human health impacts (Pedrosa, Salerno, Padilha, & Galetti, 2015; Pimentel et al., 2001; Pimentel, Zuniga, & Morrison, 2005). Therefore, signatory countries of the Convention on Biological Diversity have concentrated efforts to identify the main introduction pathways of alien species to prevent new introductions and establishments (CBD, 2014). To date, six pathways have been identified: an alien species can be introduced due to intentional release; from escapes; as a contaminant; as a stowaway within a transport vector; through anthropogenic corridors linking unconnected regions; or unaided, via other invaded regions (Hulme et al., 2008). All these pathways are directly or indirectly associated with human activities. The expansion of international commerce and commodities transportation, the intensification of tourism, and a number of technological advances have increased the frequency and volume of alien species introduced worldwide and, consequently, the number of successfully established species (Hulme, 2009; Meyerson & Mooney, 2007).

The increasing number of successfully established species can be explained by the increase in propagules (number of individuals and introduction events) and colonization pressures (number of introduced species) over time (Lockwood, Cassey, & Blackburn, 2005,2009). At the community level, a positive correlation between the number of introduced and established species can be expected. This occurs due to high colonization pressure, which allows at least one (or few) species to find suitable conditions for its establishment (Lockwood, Cassey, & Blackburn, 2009). Furthermore, the impact of colonization pressure is itself dependent on a high propagule pressure acting on the population level (Blackburn, Lockwood, & Cassey, 2015). Numerous individuals and successive introduction events are crucial to the maintenance of small and fragmented populations (Blackburn et al., 2015). Therefore, it is essential to take into account propagule and colonization pressures when analysing the alien species richness at different temporal and spatial scales.

In the first stages of the invasion continuum (Blackburn et al., 2011), human activities facilitate the establishment of alien species through the alteration of natural environments and the increase in propagule sources (Leprieur, Beauchard, Blanchet, Oberdorff, & Brosse, 2008). Thus, socio-economic variables such as the gross domestic product (GDP), the human development index and population density represent useful indicators of colonization and propagule pressures (Leprieur et al., 2008; McKinney, 2006). These variables are good proxies of the intensity of human activities related to the extent of the transport network, environmental disturbances and land use (Auffret, Berg, & Cousins, 2014; Hulme, 2009; McKinney, 2002). Economically developed and densely populated countries often have a rich invasive fauna (Jeschke & Genovesi, 2011; Westphal, Browne, MacKinnon, & Noble, 2008). Consequently, countries with emerging economies tend to be more susceptible to new invasions (Hulme, 2015; Seebens et al., 2018).

In Brazil, an emerging economy, the introduction of wild species (native or exotic) in another region or biome is prohibited (Decree no. 6.514/2008). Nevertheless, the number of invasive amphibian species has continued to rapidly increase (Forti et al., 2017), and the presence of many alien reptiles and amphibians, including established populations, has been reported in recent years (e.g., Salles & Silva-Soares, 2010; Carvalho, Fraga, Silva, & Vogt, 2013; Fonseca, Marques, & Tinôco, 2014; Prates, Hernandez, Samelo, & Carnaval, 2016). Recent phylogenetic analyses and audio recordings have contributed to clarifying some issues, such as the geographical origin, time and cause of the introduction of certain invasive species (Prates et al., 2016; Toledo & Measey, 2018). However, an in-depth explanation of the origin, volume and cause of introductions is generally not available. Such knowledge gaps make it difficult to evaluate the extent and the sources of the problems posed by alien amphibians and reptiles.

In the course of this research, we conducted a comprehensive search to identify the alien amphibians and reptiles, invaders or not, in Brazil. We aimed to answer the following questions: (a) Which alien amphibians and reptiles are present in Brazil? (b) Where do they come from? (c) Where do they occur? (d) Why were they introduced? and (e) Which factors (spatial, climatic, anthropogenic) influence record incidences and richness of these species in Brazil? Understanding the answers to these questions is a key step to future decision-making focusing on developing strategies for preserving the native biodiversity. Considering Brazilian high diversity (partly explained by suitable climatic conditions) and the human population growth (coupled with anthropogenic expansion), we expect to reveal a previously unknown exotic diversity and be able to identify the key causes of its distribution.

2 | METHODS

2.1 | Species data

We collected data about alien amphibians and reptiles in Brazil, including all alien species found, invaders or not; that is, all the species introduced in different regions of Brazil, belonging to all stages of invasion, from the transport to the spreading (see Blackburn et al., 2011). In this way, we draw attention to invasive species, and many other alien species that are in all types of stages, which may eventually spread and become invasive. We conducted a research in several sources: scientific literature, unpublished dissertations and theses, congress summaries, technical and legal governmental documents, zoological collections, online databases and expert information. We performed a systematic review using the online library databases (ISI Web of Science, Google Scholar, Scopus and Periódicos CAPES) to assess scientific papers containing terms related to amphibians and reptiles ("Amphib*"; "Reptile"; "Testudines"; "Crocodylia"; "Snake"; "Lizard"; "Anura") and variations of terms connected to invasion biology ("exotic"; "inva*"; "alien"; "non-native"; "introduc*"; and "non-indigenous") in all the available fields including the title, abstract, topic and full text. All search combinations were performed in Portuguese and English. The search began in June 2016 and was completed in July 2017. Over this time, 165 studies were discovered in total (see all studies used in the review in Supporting Information Appendix S3).

We also surveyed data from newspaper articles and websites. Although unusual, these are strategic sources to track alien species that have been illegally traded or raised as pets, and we strongly defend their inclusion in this study: first, because they are needed to describe the scenario we are trying to assess, and second, because these data are important for scientific knowledge and, especially, for environmental agencies. We carefully checked these records before including them in our dataset: they were peer-reviewed by four taxonomists from different institutions, and only specimens that they confirmed were included. A search was performed on Google using the keywords "sedex" (Brazilian postal package service); "post offices"; "confiscation"; "rescue"; "captivity"; "trafficking"; "illegal breeding"; "exotic animals"; and the common names of certain animal groups: "lizards," "anurans," "snakes," "turtles," "salamanders," and "crocodilians." This search occurred during the same period in which we revised scientific journals and collections. We only took into consideration the information found on the websites of experts NGOs, corporations and state governments, federal autarky and traditional/high-circulation regional newspapers. We ultimately included a total of 75 sources with photographs of the species in question. More details on the methodology applied to each source type and the taxonomists consulted can be found in Supporting Information Appendix S1.

Our final list is comprised of records of alien amphibians and reptiles collected from these different sources. Only species found in lists of the Brazilian Society of Herpetology were considered native to Brazil (Costa & Bérnils, 2018; Segalla et al., 2016). The nomenclature was based on the databases compiled by Frost (2017) and Uetz, Freed, and Hoek (2017). Our analyses only included records that could be associated with a valid taxonomic unit. We removed all records that merely identified a taxon as a "snake" or a "lizard" and those in which the name used represents more than one species.

The following details were noted from each record: species origin (continent/region), introduction cause, municipality of occurrence, environment type (either undetermined; natural, when inside conservation units or large native fragments; or anthropic, when the record came from urban, peri-urban and rural areas), number of individuals, and whether or not it was a confiscation record. We used municipalities as geographical units instead of grids or pixels due to two main reasons: the great variety of scales describing the locality of records across studies and the fact that socio-economic data are reported at this scale. The centroid of the municipality was standardized as a geographical unit for each record and georeferenced with Google Earth (7.1.8.3036, Google Inc.). If the total number of individuals was not available or was inaccurate (e.g., "abundant," "several"), we standardized the total value to the minimum of one individual (see Supporting Information Appendix S2). Natural distributions were extracted from The Reptile Database (Uetz et al., 2017) and AmphibiaWeb (2017). The introduction cause was classified as one of the following: (a) accidental, when the specimen was a stowaway within a transport vector or a commodity; (b) human consumption (food); (c) biocontrol; (d) landscaping; (e) pet trade; and (f) undetermined. The classification was based on the information obtained from the original source, and therefore, the same species may have been attributed multiple routes of introduction. When the information was not available, the introduction cause was classified as "indeterminate." Species were determined to have been introduced through the pet trade when the specimens were confiscated in illegal captivity, intercepted during transportation, rescued after denunciation, voluntarily delivered, or sold through e-commerce. Because some reptiles and amphibians produce toxic substances harmful to humans, we also recorded the occurrence of species of medical importance.

2.2 | Explanatory variables

To explain the distribution of records and the richness of alien amphibians and reptiles in Brazil, we used a number of descriptor variables including spatial, climatic and anthropogenic factors, while also focusing on the introduction pathways. Spatial descriptors were obtained using the principal coordinate analysis of neighbour matrices (PCNM), transforming the pairs of geographical coordinates into a truncated distance matrix (Borcard & Legendre, 2002). This method decomposes the spatial relation between sites into orthogonal eigenvectors (spatial filtering) that maximize Moran's index of autocorrelation (Dray, Legendre, & Peres-Neto, 2006). We used the spatial filtering as spatial variables, extracted through the truncation distance of 2,887 km (Rangel, Diniz-Filho, & Bini, 2006). The potential influence of the municipality area on the number of records and the richness of alien species had no statistical significance, so it was not used in further analyses (alien richness: $R^2 < 0.001$, $F = 0.521$; $p = 0.471$; number of records: $R^2 = 0.002$; $F = 0.718$; $p = 0.397$).

The set of climatic predictors included the minimum and maximum temperatures and annual precipitation of each geographical unit. Annual means of climatic data were obtained from WorldClim 2.0 (Fick & Hijmans, 2017) at a 30 arc-second resolution (approximately 1 km^2). The human population density and the per capita GDP of municipalities were used as anthropogenic variables; the data in this section were based on the demographic census of 2010 (IBGE, 2017). Finally, we used three main introduction pathways (accidental, human consumption and pets) for reptiles and amphibians in Brazil as categorical predictors. For each geographical unit, we tallied the records related to the introduction pathways. For example, at locality "A," we found two records of pets, 10 records attributed to human consumption, and zero connected to accidental pathways. Records with introduction pathways classified as "undetermined" made up only 5.8%, and they were not included because they do not provide information on introduction causes. Other introduction pathways accounted for <2% of records and were also disregarded (biological control = 1.5%; landscaping = 0.01%). The details of the classification of introduction pathways are presented in Section 2.1.

2.3 | Data analyses

We built a theoretical model illustrating potential causal relationships explaining the distribution of alien species richness and the number of records (Figure 1a). This model assumes a hierarchical causal order between predictors in which spatial descriptors are exogenous, and all other variables are endogenous (Shipley, 2000). Specifically, we assume that spatial predictors influence the other predictors. The same is the case for climatic predictors, which influence all but the spatial predictors. Anthropogenic predictors can be influenced by the space and climate, and could, therefore, affect introduction pathways, record numbers and alien species richness. Record numbers and alien richness may only influence each other, but they can be explained by the different sets of predictors. In the graphical model, all causation hypotheses are represented by arrows that point from the "cause" to the "effect."

We tested the causal model using the analytical steps proposed by Brum, Kindel, Hartz, and Duarte (2012) (see also Brum et al., 2013). First, we performed a separate model selection procedure for each set of descriptors (spatial, climatic, anthropogenic and introduction pathways) to determine their value as predictors of (a) alien richness; and (b) the number of records. We then selected the best variables to be used in subsequent path analysis. It is important to note that spatial and climatic variables were not directly linked to our response variables so that our causation model could be simplified. Figure 1b illustrates the causal model resulting from the first step of our analysis.

The second analytical step was performing a new model selection using all the pre-selected variables to discover which are directly linked to the alien richness and number of records when they appear all combined. Obeying the causal hierarchy, we then performed successive model selections using, as response variables, the predictors directly related to alien species richness and number of records and, as explanatory variables, their respective potential predictors. This step was repeated, until we reached the anthropogenic factors, the most exogenous descriptors in our case (Figure 1b). All model selections were based on the corrected Akaike information criterion (AIC_c) (Anderson, 2008; Burnham & Anderson, 2002).

The final model is the one that best connects the causally structured variables according to our initial hypothetical model. The standardized regression coefficients (∞) were taken as path coefficients. The species richness was expressed as a square root, and the number of records was log-transformed ($\log10(x + 1)$). Transformations were necessary to improve residual distribution. All analytical steps were performed using the software Spatial Analysis in Macroecology 4.0 (Rangel, Diniz-Filho, & Bini, 2010).

3 | RESULTS

3.1 | What exotic amphibian and reptile species occur in Brazil?

We found 2,292 records of alien and invasive amphibians and reptiles in Brazil from 1955 to the present day. Of these, only 1,981 records of 136 species had complete information regarding taxonomic identification and occurrence locality and were consequently used in our analyses. Of the 136 species in these records, 101 were exotic to Brazil, while 35 were native Brazilian species occurring outside their original distribution range. The most frequently occurring alien species were different types of squamates with snakes and lizards, representing 44.1% (n = 60) and 23.5% (n = 32), respectively. Anurans had 27 species (19.8%), turtles with 12 species (8.8%), salamanders and crocodilians with 3 (2.2%) and 2 (1.4%) species, respectively (Figure 2). Fourteen species are considered of medical importance. Lizards and Anurans are the groups with highest number of records (Figure 3a).

3.2 | Where are they native to and where are they occurring in Brazil?

The majority of the alien species referenced in the records were native to South America (n = 60), followed by North America (n = 28) and Asia (n = 20; Figure 4). The highest concentration of records (82 alien species) occurred in the south-eastern (55.9%) and southern (18.8%) regions of Brazil, within the Atlantic Forest Biome (Figure 5). Nearly 45.2% of the records were made in anthropic areas, with 10%

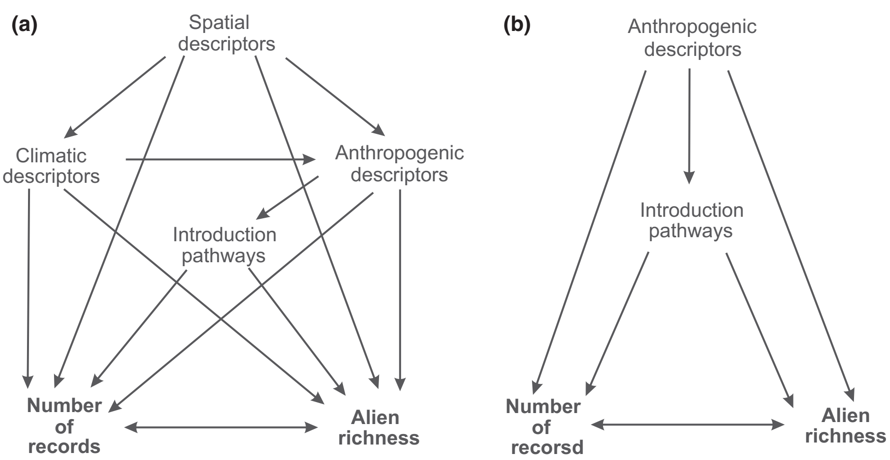


FIGURE 1 Theoretical causal model explaining the relationships between the richness of alien herpetofauna and the number of records and (a) the potential causal predictors set: spatial, climatic, and anthropogenic factors, and introduction pathways; and (b) the final path model representing the potential causal links supported by model selection

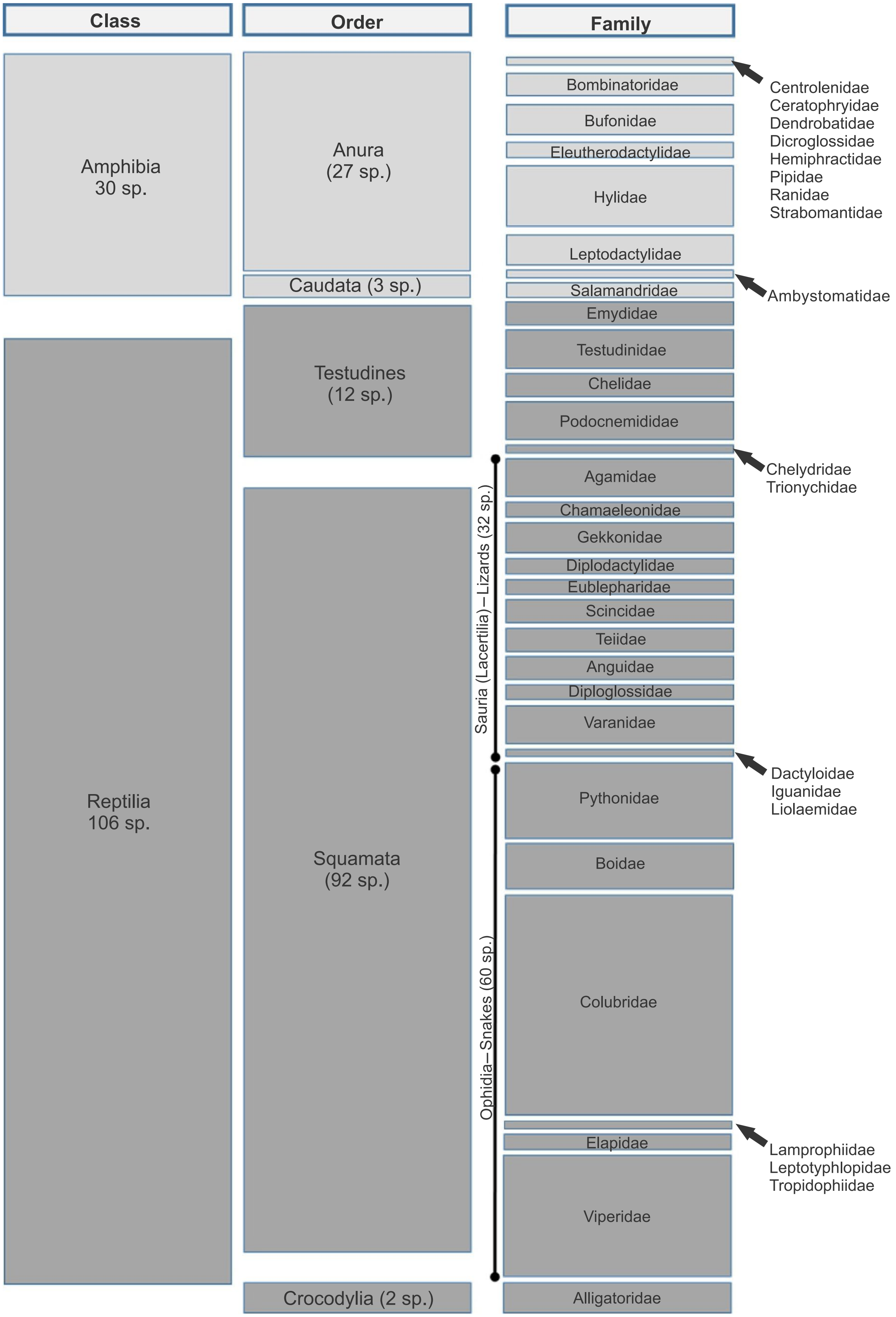
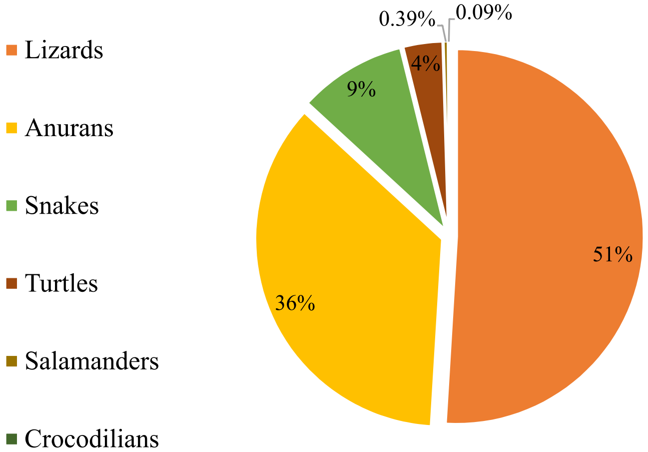


FIGURE 2 Richness and proportion of species recorded among different taxonomic groups. Bars are scaled by height to represent the number of species. Families with only one species are grouped into a single bar

(a)



(b)

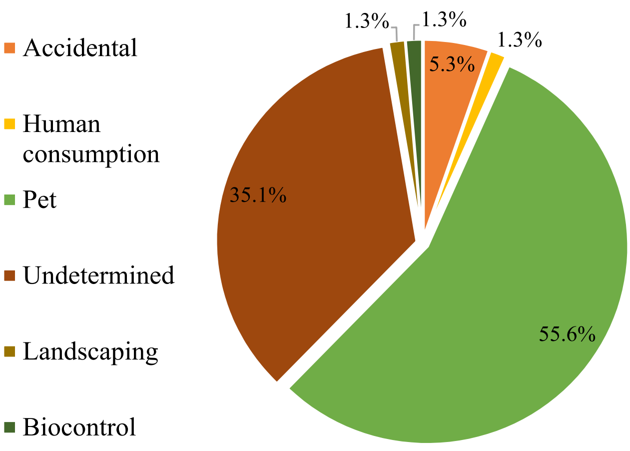


FIGURE 3 Distribution of the number of records per taxonomic group (a) and proportion of the number of species by introduction pathways (b)

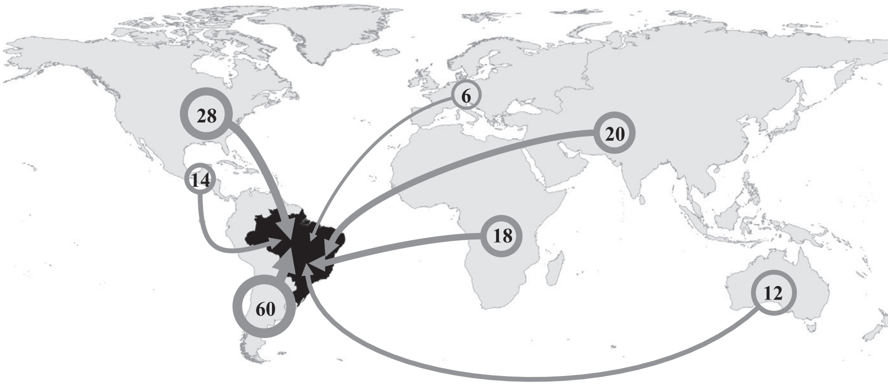


FIGURE 4 Origins and number of alien reptile and amphibian species found in Brazil by continent/region

in natural environments; 13 species were found inside conservation units. Type of environment could not be determined in 44.6% of the records.

3.3 | Why were they introduced?

The pet trade was responsible for the introduction of more than half the species (55.6%). Only 6.4% of the total records were related to confiscations; this value corresponds to 47 alien species introduced to Brazil and 19 native species that were exotic to the regions where they were found, having been trafficked or raised as pets. Accidental introductions (5.3%), introductions related to human consumption, biocontrol and landscaping (1.3% each) represented a lower percentage of the diversity of the introduced species (Figure 3b). We could not identify the introduction pathway for 39 of the observed species. Even though the species that were accidentally introduced or related to human consumption showed low diversity, they totalized most of the records (77.1%): these records mainly refer to House geckos (*Hemidactylus mabouia*; 45.7%) and American bullfrogs (*Lithobates catesbeianus*; 30%), respectively.

3.4 | Which factors best explain the record incidence and richness of these alien species in Brazil?

Anthropogenic variables and introduction pathways were selected as predictors to explain both the richness of alien amphibians and reptiles and the number of records. The model selection (presented in Table 1) did not support the importance of spatial and climatic variables (Table 1). The GDP and the pet trade presented the highest path coefficients directly explaining alien richness (Figure 6). The former also affects richness indirectly by increasing the importance of the pet introduction pathway. These pathways showed positive coefficients, indicating that most developed areas, where more pet species can be found, are characterized by higher alien richness. The number of records and the human population density also have a direct and positive influence on richness. The other introduction pathways only indirectly impact species richness through their influence on the number of records. This model explains 74% of the variation of alien richness.

The number of records was directly related to multiple factors. Higher alien richness and all three introduction pathways increased the number of records. The accidental and human consumption

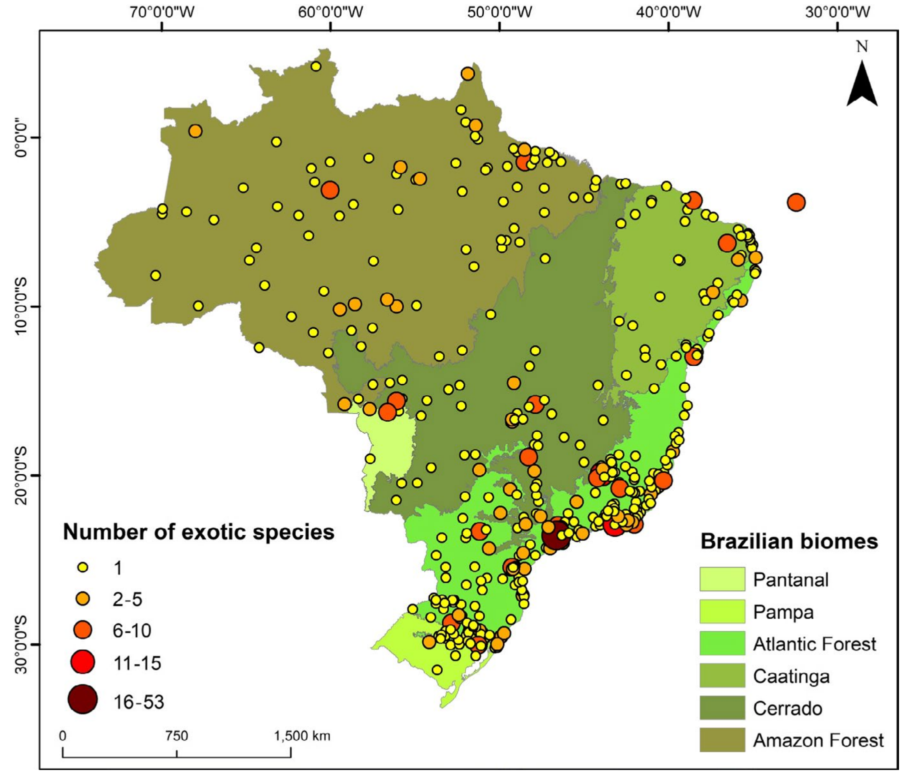


FIGURE 5 Geographical distribution of alien herpetofauna records found in Brazil across natural biomes. The circle sizes and colours reflect the number of records

TABLE 1 The best models explaining the variations of alien species richness and the number of records for the four groups of tested predictors. Selection was based on the Akaike information criterion (AIC_c) and Akaike weight (*w*). The selected models revealed the highest AIC_c, which describes the relative likelihood of the model, normalized across the set of all possible models to sum 1

Model selection	R^2	AIC_c	*w*
1. Spatial			
Richness	0.006	542.526	–
Number of records	0.032	234.823	–
2. Climatic			
Richness	0.018	538.894	–
Number of records	0.029	229.21	–
3. Anthropogenic			
Richness: population density; GDP	0.668	65.353	0.999
Number of records: population density; GDP	0.151	165.586	0.969
4. Introduction pathways			
Richness: pet; accidental	0.632	109.951	0.624
Number of records: pet; accidental; human consumption	0.675	−248.955	1

introduction pathways were the most important causal predictors of the number of records. The GDP had a positive indirect influence on this variable once it increases accidental introductions, the introductions of pets and alien species richness, which in their turn increase the number of records. However, the GDP also presented a negative direct path (Figure 6). This indicates that, overall, more developed areas tend to have more records of aliens, as there are more species, but some localities do not follow this trend. The human population density also positively affects the record numbers indirectly, by increasing accidental introductions and alien richness. This model configuration highlights the complexity of the inter-relationship between factors contributing to the distribution of records of alien amphibians and reptiles in Brazil. While pet introduction promotes higher alien richness, introduction pathways related to human consumption and accidental introductions directly increase the number of records.

4 | DISCUSSION

4.1 | Understanding alien amphibian and reptile diversity in Brazil

The identification of the alien species in a given area and the factors regulating their introduction is an important step in understanding the establishment process and defining indicators that can be used in decision-making processes. In this study, we found a surprising diversity of alien species in Brazil, native to all different parts of the world and belonging to all kinds of invasion stages. We believe that the diversity of sources used in this study enabled us to build a consistent database. This effort was essential for a broad description and analysis of the distribution and causes of alien amphibians and reptiles in the country, including historical and contemporary information. Using a causal model approach, we revealed that the pet trade and the GDP are the most influential predictors of the richness of alien amphibians and reptiles. Human population density also directly affects alien richness, with a lower path coefficient. Such results offer additional support for the hypothesis that colonization pressure and human activity are key factors in increasing alien species diversity (Leprieur et al., 2008; Lockwood et al., 2009). Our findings also revealed that explaining the distribution of records requires a larger number of causal links. Besides economic activities, all introduction pathways play important roles in determining the number of records.

The alien and invasive species found in this survey mainly consisted of snakes, lizards and anurans, echoing the richness of amphibians and reptiles established worldwide (Capinha et al., 2017). Exotic species from all continents have been introduced to Brazil, with a higher proportion of species from South and North America, followed by Asia and Africa. The predominance of species originating from South America may be related to the high diversity and socio-economic pressures inherent in developing countries, where poverty and poor infrastructure lead to inefficient inspections and biosafety, making corruption and the trafficking of animals attractive alternatives (Auliya et al., 2016; Balmford et al., 2002; Brenton-Rule, Barbieri, & Lester, 2016).

The Atlantic Forest region is characterized by the highest concentration of alien amphibians and reptiles in Brazil, and this can be explained by socio-economic factors (i.e., human population density, per capita GDP). The Atlantic Forest domain is a very large and diverse region, in which nearly 72% of the Brazilian population lives, and it is responsible for 80% of the Brazilian GDP, concentrating the most important ports and industrial, chemical and oil centres (Fundação SOS Mata Atlântica, 2016). This biodiversity hotspot also harbours the greatest diversity of alien and invasive species of plants and other animals found in the country (Sampaio & Schmidt, 2013; Zenni, Dechoum, & Ziller & S. R., 2016). Economic activities increase the flow of alien species through multiple pathways (Hulme et al., 2008), directly or indirectly determining the diversity and propagule releases and the number of introduction events (Blackburn, Lockwood, & Cassey, 2008; Cassey, Blackburn, Duncan, & Lockwood, 2005; Hulme, 2009; Meyerson & Mooney, 2007). Such a relationship was evident in our model due to the strong association between the GDP and alien richness, as well as between pet and accidental introduction pathways.

Most species and records were observed in anthropic environments, but we found 11 alien species (seven reptiles and four amphibians) in Brazilian conservation units (CUs), where the presence of other alien taxa has also been recorded (Sampaio & Schmidt, 2013; Ziller & Dechoum, 2013). Currently, studies suggest that protected areas may not be sufficient to support the long-term maintenance of biodiversity and that these regions will probably be subject to further biological invasions in the future (Araújo, Alagador, Cabeza, Nogués-Bravo, & Thuiller, 2011; Barbosa, Both, & Bastos, 2017; Loyola et al.,

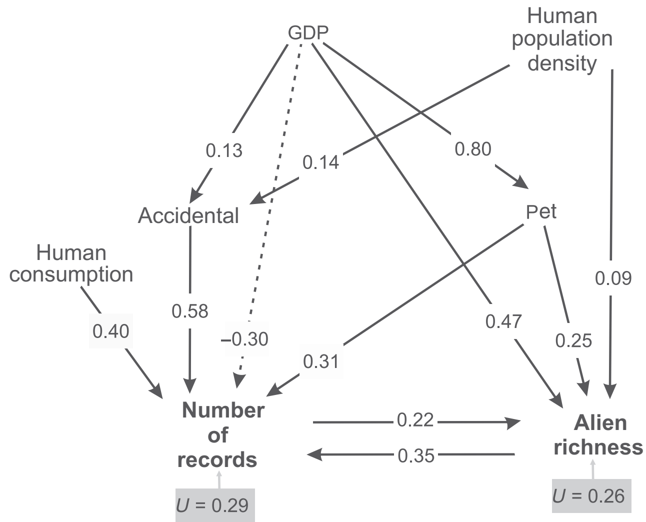


FIGURE 6 The final path model showing causal relationships between anthropogenic and introduction pathways predictors and alien amphibians and reptiles richness and number of records in Brazil. Solid arrows represent positive effects, and dashed arrows represent negative effects of the variables. Path coefficient values on the arrows are the standardized regression coefficients. Only paths with $p \le 0.05$ are included. U = non-determination coefficient presented for the endogenous variables ($U = 1 - R^2$); alien richness = number of alien species of amphibians and reptiles; number of records = amount of records; human population density = density of citizens in a given locality; GDP = gross domestic product (from municipalities); accidental, human consumption and pet = introduction pathways

2012). In Brazil, CUs are often located in or near large urban centres, surrounded by a high-density population, who sometimes illegally occupies the CU area. These situations, associated with other anthropogenic disturbances, act as propagule sources, facilitating the introduction of alien species in protected areas (Smallwood, 1994; Spear, Foxcroft, Bezuidenhout, & McGeoch, 2013; Wittemyer, Elsen, Bean, Burton, & Brashares, 2008).

In our study, we found that neither spatial nor climatic factors impact alien species richness or the distribution of records. Similarly to what other studies have found regarding fish, birds, mammals and plants (Chiron, Shirley, & Kark, 2009; Jeschke & Genovesi, 2011; Leprieur et al., 2008; Taylor & Irwin, 2004), our results indicate that anthropogenic factors are more important than natural ones in regulating the introduction of alien species, reinforcing that this may be a general pattern for macroscale analyses. The GDP was identified as an important predictor of the species richness of alien reptiles and amphibians in Brazil. This is probably due to a positive relationship between human activities and the releases of specimen/species propagules (Lockwood, Cassey, & Blackburn, 2005; McKinney, 2006). Areas where economic development and human density are elevated are expected to contain more species than those that are less developed with a lower population density.

The analysis of the introduction pathways revealed that accidental introductions and human consumption increase the number of records, while the pet trade increases alien richness. The causal model revealed that accidental introductions are the main direct factor explaining the number of records. These introductions are more likely to occur on high-intensity transportation routes, which are common in wealthy areas (i.e., those with a higher GDP) (Hulme, 2009). Here, this relationship is strongly influenced by the species *Hemidactylus mabouia*, or gecko. The gecko was probably brought to Brazil accidentally about 500 years ago on ships coming from Africa, and it is currently abundant and widely distributed throughout the country, mainly in urban areas throughout the country (Rocha, Anjos, & Bergallo, 2011). The number of records was also influenced by factors related to human consumption introduction pathway; the most evident example of this is the American bullfrog (*Lithobates catesbeianus*). This species was introduced for aquaculture purposes and is currently invasive and widely distributed throughout the country (Both, Madalozzo, Lingnau, & Grant, 2014). Bullfrogs were introduced in the 1930s, and in the following decades, individuals escaped from farms; simultaneously, they were freely distributed to rural owners by governmental agencies (Both et al., 2011; Lima & Agostinho, 1988). Due to this fact, they also occur in small municipalities and properties, typically from localities with a low GDP. In addition, our analyses revealed that the introduction of these species with high number of records and widely distributed is not related to high-populated areas or exclusive to well-developed regions.

Historical and cultural factors linked to human activities also influence alien species richness. As the causal model reveals, high-populated areas have more alien species diversity, and this is mostly due to the presence of species introduced as pets. Our results also indicate that the introduction of species through the pet trade is higher in the wealthier and more developed areas of the country. The path model indicates that the GDP is strongly associated with the introduction of pet species, which in turn increases species richness and the number of records.

4.2 | Insights into alien pet trade and future invasions

As previously stated, a high proportion of the species diversity is caused by the introduction of exotic pets. In Brazil, the importation of reptile and amphibian species (except for bullfrogs) for breeding for commercial purposes and for pet market is prohibited by Federal Order no. 93/1998. Therefore, the trade of pet species from other countries is illegal (specimens imported before 1998 cannot be sold, only donated). The commercialization of native wild species depends on the approval and supervision of each state, but all the records examined in this study were from irregular pet ownership, with no licences or identification chips. Keeping reptiles and amphibians as pets endangers the native diversity in two ways: it removes the species from their natural habitat, and it introduces alien species to different regions. The pet trade is responsible for threats, invasions and extinctions of many animal species worldwide (García-Díaz & Cassey, 2014; Kraus, 2009; Schlaepfer, Hoover, & Dodd, 2005).

The species introduced by the pet trade most often referenced in the records are the *Pantherophis guttatus* and *Trachemys scripta*, both with more than 300 introduced individuals. Currently, only *Trachemys scripta* has been confirmed to have invaded some regions of Brazil (Bujes, 2011; Silva-Soares, Ferreira, Salles, & Rocha, 2011). Although there is no evidence that there is an invasion of *Pantherophis guttatus* in progress, we believe that it is only a matter of time. Besides being the most common illegally traded species in the country (Magalhães & São-Pedro, 2012), *Pantherophis guttatus* has a high probability of establishment in Brazil (Fonseca et al., 2014; Fonseca, Solé, Rödder, & de Marco, 2017). Of particular concern is the commercialization of venomous alien species as pets, which represents a risk to public health (Minton, 1996; Schaper et al., 2009). As in most countries, only specific antivenoms for the genera of native species are available in Brazil (Ministério da Saúde Brazil, 2001). Therefore, injuries caused by alien pets can result in human death. This could occur if, for example, a person is bitten by species such as the *Naja kaouthi* (monocled cobra) that was found in an urban area of Brazil (see Supporting Information Appendix S2).

According to the "invasion debt" concept, even if the introductions stop, new invasions will continue to emerge due to a "lag" phase, in which species that have already been introduced remain in small quantities for a long time until they become invasive, and their impacts are detected (Essl et al., 2011; Richardson, 2011). Therefore, if species introduced for human consumption and through accidental introductions are already widespread and invasive in Brazil, pets pose an imminent threat. The impact of these introductions and current socio-economic activities on patterns of alien species richness will become clearer in the future.

5 | CONCLUSIONS

Our study constitutes a comprehensive and important analysis of the diversity and distribution patterns of alien amphibians and reptiles in Brazil. We were particularly surprised by the number of species from all around the world that were present in this already megadiverse country and those that had been moved across biomes. The total number of records was also high, but it was mostly composed of species that we expected to find, since they are already invasive, introduced for human consumption or accidentally. We recognize that the number of alien species is probably actually higher. Depicting the main introduction pathways was a key step in understanding how human activity affects the distribution of alien species richness and the number of records. Because the effects of many such introductions can sometimes only be observed decades later, knowing the introduction finality and routes is an important element in proposing conservation strategies that will serve to prevent the invasion of many species and the arrival of new propagules.

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DATA ACCESSIBILITY

All the original data used in this study are available in the supporting information (Supporting Information Appendix S4).

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BIOSKETCH

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Author contribution: All authors conceived the idea and contributed to the data acquisition. E.F. and C.B. have been involved in analysing and interpreting the data; E.F. wrote the first draft; all authors contributed critically to writing.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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