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Diversity, biogeography and the global flows of alien amphibians and reptiles

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Abstract

Aim: We introduce a high-quality global database of established alien amphibians and reptiles. We use this data set to analyse: (1) the global distribution; (2) the temporal dynamics; (3) the flows between native and alien ranges; and (4) the key drivers of established alien amphibians and reptiles.

Location: Worldwide.

Methods: We collected geographical records of established amphibians and reptiles from a thorough search across a wide number of sources. We supplemented these data with year of first record, when available. We used descriptive statistics and data visualization techniques to analyse taxonomic, spatial and temporal patterns in establishment records and the global flows of alien species. We used generalized linear mixed models to relate spatial variation in the number of established species richness with variables describing geographical, environmental and human factors.

Results: Our database covers 86% of the terrestrial area of the world. We identified 78 alien amphibian and 198 alien reptile species established in at least one of our 359 study regions. These figures represent about 1.0% of the extant global amphibian and 1.9% of the extant global reptile species richness. The flows of amphibians were dominated by exchanges between and within North and South America, and within Europe

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(59% of all links). For reptiles, the network of global flows of established alien species was much more diverse, with every continental region being both a donor and a recipient of similar importance. The number of established alien amphibians and reptiles has grown slowly until 1950 and strongly increased thereafter. Our generalized linear mixed models revealed that insularity, climatic conditions, and socio-economic development significantly influenced the distributional patterns for both groups.
Main conclusions: We conclude that biological invasions by alien amphibians and reptiles are a rapidly accelerating phenomenon, particularly on islands with heterogeneous climates of economically highly developed countries.

KEYWORDS
biological invasions, distribution, establishment, Global Alien Herptile Database, hotspots, temporal trends

1 | INTRODUCTION

Human activities have rapidly changed the distribution of biota at an unprecedented scale (McKinney & Lockwood, 1999) and continue to do so. Ever increasing numbers of species are transported by humans into areas outside their natural ranges (van Kleunen et al., 2015), which results in profound changes of biogeographical patterns (Capinha, Essl, Seebens, Moser, & Pereira, 2015). These alien species impact on native biodiversity due to competition, predation and hybridization and act as vectors of pathogens and diseases dangerous to both humans and other wildlife (Hof, Araújo, Jetz, & Rahbek, 2011). Alien species also have major economic and social impacts that directly and indirectly affect human welfare (Kumschick et al., 2015; Vilà et al., 2011). Although research in biological invasions has intensified over the last decades, major taxonomic and geographical knowledge gaps still remain, and global analyses of invasion patterns are still missing for some groups of organisms. This limits a comprehensive understanding of mechanisms and patterns of invasions at large scales (Pyšek et al., 2008; Richardson & Ricciardi, 2013) and, in turn, prevents the implementation of sound preventive response actions.

The two vertebrate groups considered here, amphibians (c. 7,635 extant species; Frost, 2017) and reptiles (c. 10,450 extant species; Uetz & Hallermann, 2016), are ancient phylogenetic groups with a worldwide distribution, absent only from very isolated oceanic islands and cold environments. Data on the global distributions of alien amphibians and reptiles are becoming increasingly available, and there is evidence of substantial impacts on native biota (Kraus, 2015), but a global synthesis on both the distribution and the temporal patterns of established alien species is still lacking. Previous studies, in particular the seminal work by Fred Kraus (Kraus, 2009), have provided a comprehensive collection of introduction events of amphibians and reptiles on a global scale and have yielded valuable insights into the introduction dynamics of these taxonomic groups. However, comprehensive analyses of the global distribution, flows and drivers of establishment of alien amphibians and reptiles are still lacking. Moreover, in recent years, there have been substantial updates on alien amphibian and reptile distributions (e.g., DAISIE, 2015; Edgar, 2015; García-Díaz, Ross, Ayres, & Cassey, 2015; Powell et al., 2011; Soubeyran, Caceres, & Chevassus, 2011), which require analysis collectively in a global context.

Here, we present the recently completed Global Alien Herptile Database, a comprehensive database of alien amphibian and reptile distributions in countries, federal states and biogeographically separated islands or archipelagos worldwide. We focused on established alien species, defined as those that do not occur naturally in a region and form self-sustaining, introduced populations in that region (Blackburn et al., 2011). We excluded casual (i.e., not permanently established) occurrences. Our database contains the distribution of established alien amphibians and reptiles in 359 regions. In a subsequent step, we use this data set to analyse: (1) the global distribution of established alien amphibians and reptiles, (2) the flows of established alien species between their native and alien ranges, (3) the temporal dynamics of invasions during the last centuries and (4) the key drivers shaping the richness of established alien amphibian and reptile species at the global scale.

2 | METHODS

2.1 | Study region selection

We used the Biodiversity Information Standards (TDWG) World Geographical Scheme for Recording Plant Distributions version 2.0 (http://www.kew.org/gis/tdwg/index.html) for region delineation. This classification scheme was developed as a standard delineation of the world for biogeographical analyses, and we have adopted it here as our geographical reference to make our analyses readily comparable between the two taxonomic groups. We used level 4, which contains 608 geographical units; these correspond to countries, federal states of large countries and biogeographically separate islands or archipelagos. We consider this level of spatial resolution appropriate for studying biogeographical patterns on a global scale, and it also represents the highest feasible spatial resolution as many alien species data are reported on national or federal state levels. We additionally included country-level data for a few countries for which species data were not available at the spatial scale of TDWG level 4. These countries were Brazil, Chile, China, India, Indonesia, Japan, New Zealand, Russia and the United Kingdom. Region size varies between approximately 17,000,000 to 0.5 km^2 for continental regions (median: 118,073 km^2) and between about 1,900,000 to 0.03 km^2 for island regions (median: 703 km^2).

2.2 | Species data

The taxonomic species names were taken from Frost (2017) for amphibians and from Uetz and Hallermann (2016) for reptiles. We only included taxa on the species level in the analysis because of inconsistent taxonomic treatment and poor data coverage of intraspecific taxa.

We gathered distribution data from all relevant sources we could find and supplemented them with further information on introduction history (year of first record, if known). Finally, we contacted regional experts (see Acknowledgements) who checked the data set and provided additional data. Despite our best efforts, data gaps in alien herptile species distributions remain for some regions, particularly in parts of sub-Saharan Africa and the Near and Middle East.

Based on the terminology proposed by Blackburn et al. (2011), alien amphibians and reptiles were classified for each region according to their invasion status as casuals (only small, non-self-sustaining populations), established (at least one persisting, breeding population) or unknown (if an assessment of the invasion status was not possible). This assessment was undertaken based on the information provided in the data sources (n = 347; see Appendix S1) and matches the criteria adopted by Kraus (2009, p. 136) to define an introduction as being successful. When conflicting information was found in the data sources, we based our classification on the following criteria: (1) the quality and the level of detail of the data provided by the data source, and (2) the year of publication (i.e., more recent publications were given higher weight than to older ones). Only occurrences of established populations have been kept, as casual occurrences are poorly recorded in many regions, and thus, these data would have a strong recording bias. Similarly, occurrences of unknown invasion status had been excluded.

The seminal study by Kraus (2009) represents a comprehensive data set on alien herptile introductions, and it served as a base for constructing our database. We have included substantial updates on alien amphibian and reptile distributions that have become available in recent years (e.g., DAISIE, 2015; Edgar, 2015; García-Díaz, Ross, Woolnough, & Cassey, 2016; García-Díaz et al., 2015; Powell et al., 2011; Soubeyran et al., 2011). Moreover, alien species invasion statuses are notoriously dynamic; thus, a number of species which were reported as not established by Kraus (2009) have meanwhile spread and become established, such as the snake *Pantherophis guttatus* (Linnaeus, 1766) in Brazil (Fonseca, Marques, & Tinôco, 2014). We therefore reassessed every record provided by Kraus (2009) and only included those records for which evidence of establishment could be found.

For the purposes of our work, we aimed to analyse the global patterns of alien amphibian and reptile establishment and, therefore, we considered only species in our database that were alien to the whole of our study regions. This is an important distinction between our data set and that of Kraus (2009), as the latter also considers species native to certain areas of a region that have been introduced to other sites within the same region. For instance, of the seven herptiles listed as established for South Africa by Kraus (2009), five are native in this country [*Amietophrynus gutturalis* (Power, 1927); *Geochelone (Geochelone) pardalis* Fitzinger, 1835; *Hemidactylus mabouia* (Moreau de Jonnès, 1818); *Lygodactylus capensis* (Smith, 1849); *Pachydactylus bibronii* Boulenger 1885: 201]. As another example, of the five herptiles given as established for Austria by Kraus (2009), three are native [*Emys orbicularis* (Linnaeus, 1758), *Bombina bombina* (Linnaeus, 1761), *Podarcis muralis* (*Laurenti*, *1768*)], but there have been releases of non-native subspecies which have become established (in the case of *Emys orbicularis* and *Podarcis muralis*; Essl & Rabitsch, 2002). Of the remaining two alien species, *Testudo hermanii* Gmelin, 1789, is not established, and only *Trachemys scripta* (Schoepff, 1792) is established. Our approach of including only species that are alien to the entire study region follows other recent studies of other taxonomic groups such as Pyšek et al. (2010), Capinha et al. (2015), van Kleunen et al. (2015), Blackburn, Delean, Pyšek, and Cassey (2016) and Dyer et al. (2017). Our database (supplied in Appendix S1) considers the lack of any alien amphibian or reptile species in a region; that is, it includes records of regions that do not have any known established aliens.

Finally, we note that in some cases the assessments of different authors on the established alien status of amphibians or reptiles differ. We critically evaluated conflicting opinions on available data based on a range of criteria. These included the level of accuracy provided in the original data source, and the year of publication (i.e., we gave higher weight to more recent publications than to older ones). Finally, we gave particular weight to the opinion of taxonomic or region experts on the status of a species in a region. In cases of conflicting evidence, we were conservative; that is, we did not include such records in our database.

2.3 | Explanatory variables

We used a total of nine explanatory variables encompassing geographical, biotic, climatic and human influence factors to explain the variability in the number of alien amphibians and reptiles per region. These variables were as follows: (1) insularity, that is whether the region is an island (yes/no); (2) total area of the region (log10-transformed); (3) distance to mainland; (4) richness of native amphibians; (5) mean annual temperature; (6) mean annual precipitation; (7) climatic diversity; (8) total human population; and (9) per capita gross domestic product (GDP; Table S2). Geographical variables (1–3) resulted from GIS measurements using the polygon shapefiles of TWDG level 4 and of the GADM database of Global Administrative Areas (http://nwww.gadm.org/) for the countries not included in TWDG level 4. Richness of native amphibians was based on data from the IUCN Red List Spatial Data (http://www.iucnredlist.org/) and corresponded to the sum of all ranges of occupancy of native extant species overlaying each region. Climatic annual means were calculated based on the spatial data sets of the WorldClim project (http://www.worldclim.org/) at a resolution of 30 arc sec (*c*. 1 km × 1 km) for the period 1950 to 2000. Climatic diversity corresponded to the total number of distinct bioclimatic types defined by the global environmental stratification (GEnS) data set (Metzger et al., 2013). This variable is strongly correlated with within-region range of mean annual temperatures (Pearson's correlation of 0.8) and moderately with within-region range of mean annual precipitations (Pearson's correlation of 0.64). Total human population size was calculated based on population count data per grid cell in 2010, as supplied by the Gridded Population of the World, version 4 (GPWv4; http://www.ciesin.columbia.edu/data/gpw-v4/). Data on per capita GDP were taken from Ghosh et al. (2010), Gennaioli, La Porta, De Silanes, and Shleifer (2014), the Instituto Nacional de Estadística (www.ine.es/), The Worldbank (http://data.worldbank.org/), The World Factbook (https://www.cia.gov/library/publications/the-world-factbook/index.html), the United Nations Statistics Division (http://unstats.un.org/) and the Worldatlas (http:// www.worldatlas.com). No strong correlations exist between the explanatory variables, considered as an absolute Pearson's correlation coefficient value of 0.75 or higher.

2.4 | Data analyses

Statistical analyses were conducted in the R software environment for statistical and graphical computing (R Development Core Team, 2015). We used generalized linear mixed-effects models (GLMMs) in which we included "sovereign state" (i.e., the independent nation to which the region belongs to), as a random-effect term to account for the non-independence in the observations that arise from some regions sharing the same or similar political administration and legal rulings (e.g., the federal states of the USA). We fitted these models using the Automatic Differentiation Model Builder GLMMADMB package for R which provides a framework to model over-dispersed data and zero inflation (Bolker, Skaug, Magnusson, & Nielsen, 2012), two features that are found in our response variables (Table S1 in Appendix S2). We used separate GLMMs to explain variations in alien amphibian and reptile species richness, respectively. We included the full set of explanatory variables in each of the models (Table S2 in Appendix S2), with the exception of the variable representing richness of native amphibians, which was used only in the model for this species group; for reptiles, an analogous explanatory variable was not available due to lack of native species data at the spatial resolution of our data set. To aid models' numerical stability and comparison of calculated coefficients, all explanatory variables were standardized (centred and then divided by the standard deviation). For the particular case of distance to mainland, this standardization was performed based only on the values for islands, while for mainland observations their constant value of zero was retained. A few regions (28; 7.8% of total) could not be used for model fitting due to unavailable data for some explanatory variables.

For each of the GLMMs, we tested both a Poisson and a negative binomial distribution and, in all cases, the latter distribution produced a better fit to the data, as assessed by lower AIC values (732.4 vs. 730.7 for amphibian richness and 1151.5 vs. 1138.2 for reptile richness, respectively). To assess potential fit problems caused by spatial autocorrelation, we built correlograms showing the correlation among Pearson's residuals of regions over a range of geographical distances. Geographical distances between regions were calculated using the geographical centroid of each region. For both GLMMs, the correlograms indicated that spatial autocorrelation is not important (Fig. S1 in Appendix S2). These analyses were complemented by Mantel tests analysing the total correlation between the differences in Pearson's residuals and the geographical distances between regions. Likewise, no evidence of correlations were found (Mantel coefficients for all models were $|r| < .01$). Correlograms and Mantel tests were performed using the package NCF for R.

The first record of a species denotes the year when the species was detected for the first time in a given region (mainlands and islands). The first records of alien amphibians and reptiles were taken from a recently established global database of first records of alien established species of various taxonomic groups (Seebens et al., 2017). We selected only those species matching the entries in the Global Alien Herptile Database. The geographical resolution between databases differed and first records were only available on a coarser geographical scale with no subnational units of large mainland countries (Fig. S2 in Appendix S2). For example, first records were only available for total mainland area of USA and Oceanic Islands, but not for federal states of the mainland USA.

The flow diagrams of exchanged species used the geographical delimitation of the TDWG continents (Table S4 in Appendix S2) and were created using the R package CIRCLIZE, following the instructions of Sander, Abel, Bauer, and Schmidt (2014).

3 | RESULTS

A total of 78 amphibian and 198 reptile species have become established outside their native ranges (1,030 species-region establishment records altogether) in at least one of the 359 regions of the Global Alien Herptile Database, which cover 86% of the global terrestrial area (Figure 1). These figures represent about 1% of the extant global amphibian and 1.9% of the extant global reptile species richness. The great majority of established alien amphibians are anurans (frogs and toads), totalling 65 species, while caudates (salamanders and newts) are only represented by 13 species (Fig. S3 and Table S3 in Appendix S2). However, in relative terms, accounting for the global number of extant species in each group, caudates are more often found outside their native range, with 1.9% of all species being established aliens vs. only 1.0% in anurans. For reptiles, most aliens are squamates (snakes and lizards; 162 species), followed by testudines (turtles; 35 species) and crocodilians (one species) but, relative to the global species richness of each of the groups, turtles more often established as aliens (10.2%), followed by crocodilians (4.2%), and snakes and lizards

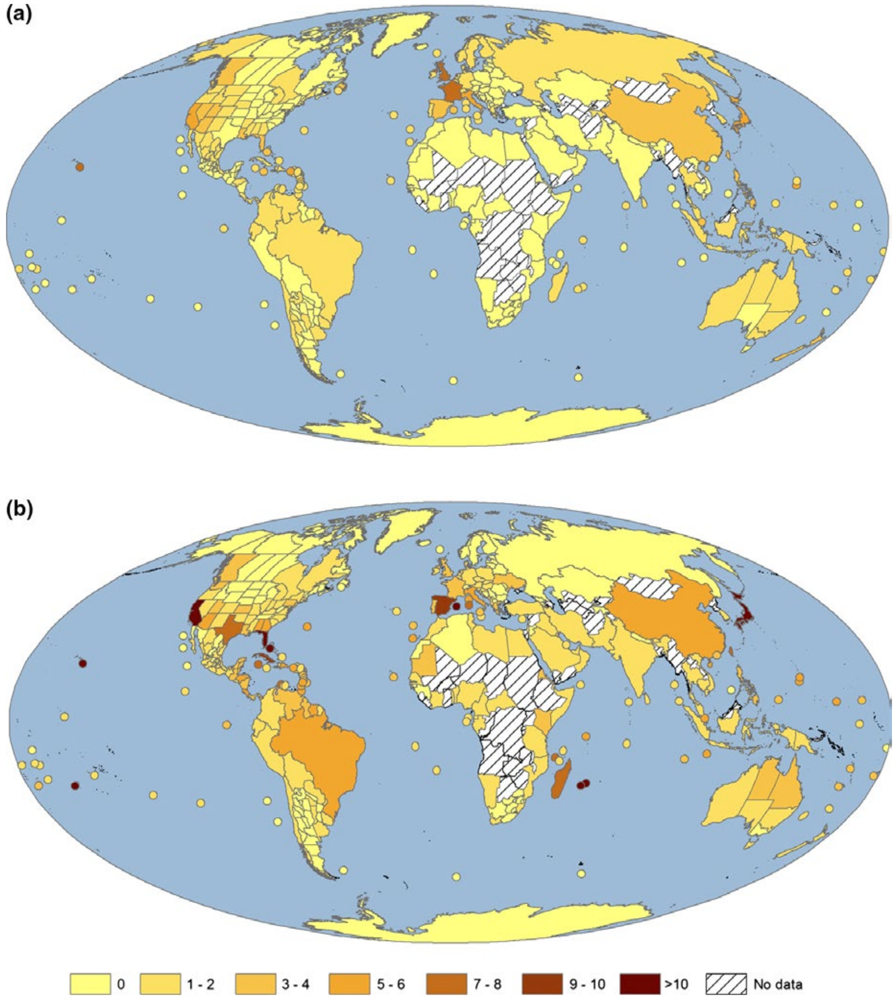

FIGURE 1 Number of established alien amphibians (a) and reptiles (b) in the 359 regions of the Global Alien Herptile Database. [Colour figure can be viewed at wileyonlinelibrary.com]

(1.6%) (Table S3 in Appendix S2). The most widely established species is the Brahminy blind snake (*Ramphotyphlops braminus* Nussbaum 1980; 83 regions), followed by the pond slider (*Trachemys scripta*; 73 regions), the common house gecko (*Hemidactylus frenatus* Duméril & Bibron, 1836; 64 regions) and the North American bullfrog [*Lithobates catesbeianus* (Shaw, 1802); 59 regions] (Table 1). Alien reptiles have substantially more establishment records (758 records = 73.6%) than alien amphibians (272 records = 26.4%). There are only 17 regions (4.7% of the total number of regions sampled) where at least 10 alien established amphibian and reptile species are recorded (Table 2). The top three regions are federal states of the USA, with Florida (58 species) ranking first, followed by Hawaii (32 species) and California (21 species). Notably, the top invaded region, Florida, hosts a large percentage (27%) of all known established alien reptile species. The geographical pattern of alien amphibian richness is reasonably similar to that of reptile richness (moderately correlated: Pearson's $r = .48$, $p < 0.001$; Figure 1).

Negative binomial generalized linear mixed models (GLMMs) show that for both amphibians and reptiles, islands are significantly richer in established alien species numbers than regions on continental land masses (Table 3). Additionally, the climatic diversity of the region and per capita GDP, as a measure for the level of socio-economic development, are positively correlated with established alien amphibian and reptile species richness. Prevailing climate was also found to be of importance, with significantly higher numbers of alien reptiles in warmer regions, and higher alien amphibian richness in wetter regions. Finally, the species richness of established alien amphibians and reptiles increases with the size of the region. All other tested variables (Table 3) show no statistically significant effect on either group.

The networks of global flows of established alien species differ between amphibians and reptiles in the direction of exchanges between continental regions (Figure 2). The flows of amphibians are clearly dominated by exchanges between and within North and South America, and within Europe (59% of all links). For reptiles, the network of global flows of established alien species is much more diverse than that of amphibians, with every continental region (except Antarctica) being both a donor and a recipient of similar importance (Figure 2). Intracontinental exchanges were less frequent (27%) compared to amphibians (38%). For reptiles, Asia and Africa represent the major donor regions, with North and South America being the most important recipient regions.

For 334 species-region records (32% of the total), information on when the species was first recorded in the given region was available.

TABLE 1 The six amphibian and 11 reptile species, which are established in at least 10 regions of the Global Alien Herptile Database

Species		Regions invaded
Ramphotyphlops braminus	Reptile (Sq)	83
Trachemys scripta	Reptile (Ts)	73
Hemidactylus frenatus	Reptile (Sq)	64
Lithobates catesbeianus	Amphibian (An)	59
Hemidactylus mabouia	Reptile (Sq)	43
Hemidactylus turcicus	Reptile (Sq)	36
Rhinella marina	Amphibian (An)	36
Lepidodactylus lugubris	Reptile (Sq)	18
Anolis sagrei	Reptile (Sq)	17
Podarcis siculus	Reptile (Sq)	16
Tarentola mauritanica	Reptile (Sq)	16
Gehyra mutilata	Reptile (Sq)	15
Eleutherodactylus johnstonei	Amphibian (An)	13
Xenopus laevis	Amphibian (An)	12
Eleutherodactylus planirostris	Amphibian (An)	10
Hemidactylus garnotii	Reptile (Sq)	10
Osteopilus septentrionalis	Amphibian (An)	10

Taxonomic orders are given in parentheses: Anura (An); Squamata (Sq); Testudines (Ts).

The numbers of first records per 20-year periods increased steadily during the past three centuries for both amphibians and reptiles (Figure 3), and accelerated during 1960–2000 when 38% and 61% of all their first records, respectively, occurred. The locations of the regions where the species were detected first during the last centuries were widely scattered around the globe with a tendency of more first records found in the Northern Hemisphere in recent decades (Figure 3). Only two species are known to have established into any of our study regions prior to 1800. These earliest records refer to amphibians and are reported from Mauritius [*Ptychadena mascareniensis* (Dumeril & Bibron, 1841), in 1769] and Canary Islands [*Pelophylax perezi* (López-Seoane, 1885)].

4 | DISCUSSION

Our assessment shows that the percentage of the total extant species numbers of amphibians and reptiles that have become established anywhere outside their native range (1% and 1.9%, respectively) is lower than that of vascular plants (3.9%) (van Kleunen et al., 2015) and mammals (2.6%) (Clout & Russell, 2008), and considerably lower than the percentage for birds (>6%) (Cassey, Vall-Llosera, Dyer, & Blackburn, 2015). Thus, the relative level of establishment of alien amphibian and reptile species at a global scale remains moderate to date, although we found distinct spatial variation among national and subnational geographical units.

TABLE 2 The 17 regions in the Global Alien Herptile Database with a minimum of 10 established alien amphibian and reptile species

No	Region	Established alien amphibians	Established alien reptiles	Total
1	Florida (USA)	4	54	58
2	Hawaiian Is. (USA)	7	25	32
3	California (USA)	6	15	25
4	Baleares Is. (SPA)	3	17	20
5	Japan	5	12	17
6	Mauritius	2	15	17
7	Bahamas	4	11	15
8	Réunion	2	13	15
9	Cook Is.	0	14	14
10	Spain (mainland)	4	9	13
11	Guam	5	6	11
12	Italy (mainland)	5	6	11
13	Puerto Rico	6	5	11
14	Cuba	1	9	10
15	France (mainland)	7	3	10
16	Taiwan	3	7	10
17	United Kingdom	7	3	10

Our analyses revealed that the regional numbers of established alien amphibian and reptile species are positively associated with human pressure (per capita GDP). Several large-scale studies show that proxies of socio-economic development (such as per capita GDP) are important correlates of alien species richness (e.g., Essl et al., 2011; Jeschke & Strayer, 2005; Pyšek et al., 2010), and this is especially true for established alien amphibians and reptiles, which are typically moved around the world by the pet trade or as stowaways (Helmus, Mahler, & Losos, 2014). The relationship between GDP and alien species richness may be confounded by a sampling bias towards rich countries with more intense sampling. However, the hotspots of alien species richness observed here are similar to those found for other well-investigated taxonomic groups such as birds (Dyer et al., 2017) and vascular plants (van Kleunen et al., 2015) with highest alien species numbers in large economies. The congruence in the distribution of alien species across these studies indicates that the patterns observed here are likely to be true and not due to a biased sampling intensity.

Another result from the statistical analysis is that the numbers of established alien amphibians and reptiles on islands are on average significantly higher than in continental regions. Higher alien species richness on islands is known to be a consistent feature for most, if not all, plant and animal taxonomic groups analysed so far (e.g., Denslow,

TABLE 3 The negative binomial generalized linear mixed models (GLMMs) explaining the number of established alien amphibian (A) and reptile (B) species per region

Explanatory variable	Coefficient (SE)	*p*
(A)		
Intercept	−1.148 (0.159)	**<.001**
Geographical variables		
Insularity (Yes)	1.603 (0.208)	**<.001**
Area (log_{10})	0.316 (0.132)	**.017**
Distance to mainland	−0.155 (0.08)	.053
Biotic variables		
Richness of native amphibians	−0.091 (0.09)	.309
Climatic variables		
Mean annual temperature	0.176 (0.101)	.083
Mean annual precipitation	0.198 (0.1)	**.048**
Climatic diversity	0.51 (0.103)	**<.001**
Human-related variables		
Total human population	−0.066 (0.069)	.332
GDP per capita	0.44 (0.09)	**<.001**
(B)		
Intercept	−0.097 (0.11)	.378
Geographical variables		
Insularity (yes)	1.07 (0.168)	**<.001**
Area (log_{10} transformed)	0.291 (0.1)	**.002**
Distance to mainland	0.037 (0.049)	.456
Climatic variables		
Mean annual temperature	0.676 (0.086)	**<.001**
Mean annual precipitation	0.057 (0.065)	.38
Climatic diversity	0.35 (0.075)	**<.001**
Human-related variables		
Total human population	−0.05 (0.057)	.38
GDP per capita	0.346 (0.07)	**<.001**

Models used a total of nine explanatory variables as fixed effects, all standardized to zero mean and standard deviation of one. After removal of cases with missing values, a total of 331 regions were used for model fitting (i.e., about 92% of all regions in the Global Alien Herptile Database). Random-effect intercept terms with sovereign state to which each region belongs to as grouping factor (see section 2) account for historical and political non-independence of the data. Significant relationships are shown in bold ($p < 0.05$).

Space, & Thomas, 2009; Duncan, Blackburn, & Sol, 2003; van Kleunen et al., 2015), with differing levels of invasion being closely related to the extent of human impact on island ecosystems (Blackburn et al., 2016; Denslow et al., 2009; Kueffer et al., 2010). Finally, climatic variables are highly relevant in explaining the biogeography of amphibian and reptile invasions. Interestingly, climatic heterogeneity is more important than mean temperature or precipitation, especially for amphibians, indicating that climatic diversity of a region, which increases the diversity of habitats and thus ecological niches available, is crucial for the establishment of alien amphibians and reptiles. Native species richness was not found to be a significant predictor for amphibians, likely because of the mismatch between hotspots of native species richness located in (sub)tropical regions and those of alien species richness, which are mostly found in temperate regions.

The origins and flows of established alien species clearly differ between amphibians and reptiles. Most established alien amphibians originate from North and South America, the latter being the hotspot of global native amphibian diversity (Hof et al., 2011). Such high species diversity combined with strong socio-economic pressures, such as trade and tourism particularly in the United States, increases the chance of moving amphibians to other parts of the world. However, the intercontinental exchanges of amphibians are dominated by a flow of established alien species from North to South America, the latter including Central America in the TDWG classification, with 70% of these exchanges representing introductions to islands in the Caribbean. Invasions of alien amphibians from the United States and Mexico to the Caribbean islands seem likely as the oceanic barriers between these two areas hindered natural exchanges in the past, while this barrier weakened in recent times due to intensified trade and many tourists visiting the Caribbean (Helmus et al., 2014). Our results on the high intracontinental exchanges within North America and Europe reflect the fact that these two continents are among the top pet-trade regions globally, especially also for pets taken from the wild (Robinson, Griffiths, John, & Roberts, 2015; Schlaepfer, Hoover, & Dodd, 2005; Warwick, 2014). In contrast to amphibians, the global hotspots of species richness of reptiles are more evenly distributed in (sub)tropical regions worldwide (Kier et al., 2009), which may explain the higher diversity of source regions of established alien reptiles (Figure 2). As popular pet animals, reptiles are commonly transported in large numbers around the globe (García-Díaz et al., 2015) either directly or indirectly. For example, species such as the pond slider (*Trachemys scripta*), the second most widely distributed established alien reptile, are frequently kept as pets. On the other hand, the fossorial and parthenogenetic small Brahminy blind snake (*Ramphotyphlops braminus*), the most widely dispersed alien reptile, has been accidentally introduced as "contaminant" predominantly via the nursery plant trade (McDiarmid, Campbell, Touré, & Shaka, 1999).

One major difference between alien reptiles and amphibians is that the former group is richer in established species, both in absolute and relative terms. This difference likely reflects the higher number of introduction events for reptiles in the past (Kraus, 2009; Smith et al., 2009), and particularly for turtles, which are characterized by the highest proportion of aliens among all orders examined in our study (35 species; c. 11% of extant species). Likewise, families popular in the pet trade (e.g., Iguanidae), or living in close association with humans (e.g., Gekkonidae), also have disproportionally high numbers of established aliens (both groups with 32 species; c. 76% and 3% of extant species, respectively). This result is consistent with findings from other taxonomic groups such as birds (Dyer et al., 2017). Altogether, these results suggest that biogeographical patterns in alien amphibian and reptile species richness are linked to variations in propagule pressure, which are likely modified on the level of individual species by factors such as advantageous biological traits (García-Díaz et al.,

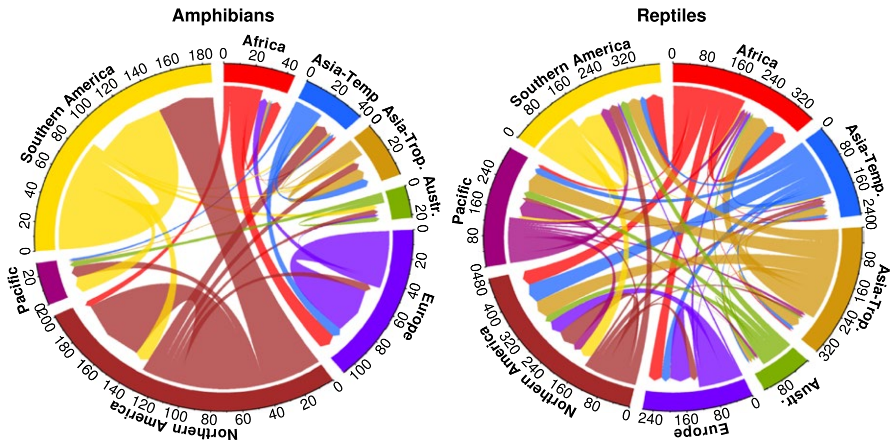

FIGURE 2 The global exchange network of alien amphibians and reptiles. Shown are the directed flows of established alien amphibians and reptiles from native to alien TDWG continents. Colours indicate the TDWG continents, where the species are native. The size of the links denotes the number of establishments (rather than the number of species). Thus, the same species may be counted multiple times if it originates from multiple regions or established in multiple regions. The size of the outer circle segments indicates the total number of establishments in or originating from that region. [Colour figure can be viewed at wileyonlinelibrary.com]

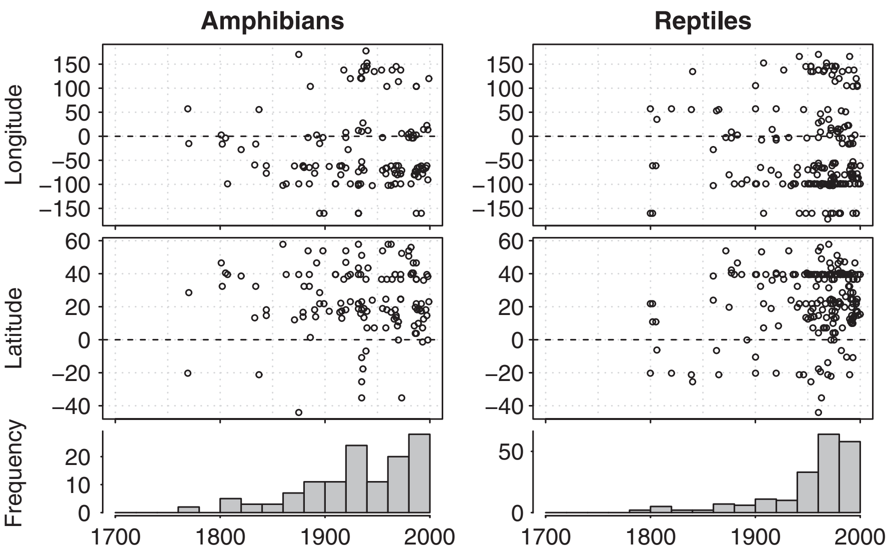

FIGURE 3 Temporal development of longitudes and latitudes of first records of amphibians and reptiles that later became established in a region worldwide. The coordinates represent the centroids of the respective regions. The histograms show the temporal development of the number of first records in 20-year periods

2016; Mahoney et al., 2015) as shown for other taxa (Capellini, Baker, Allen, Street, & Venditti, 2015; Pyšek et al., 2015; Sol, Bacher, Reader, & Lefebvre, 2008).

In comparison with the data set provided by Kraus (2009), our database contains fewer alien species. This is mostly due to our focus on established alien species and our deviating categorization of what is considered to be an established alien species in a region, which is in line with studies about other taxonomic groups such as vascular plants (van Kleunen et al., 2015; Pyšek et al., 2010), birds (Blackburn et al., 2016; Dyer et al., 2017) and gastropods (Capinha et al., 2015). As another important difference to the data set provided by Kraus (2009), we substantially updated the records from newly available sources. Indeed, 21% of records for amphibians and 29% for reptiles were obtained from sources available after the book by Kraus (2009), and another 48% (amphibians), respectively, and 42% (reptiles) of records were retrieved from online sources (e.g., databases) that contained many new entries in recent years (Table S1 in Appendix S2). Altogether, this led to a genuinely novel and distinct database of alien amphibian and reptile distributions.

The number of first records of establishment increased continuously during the last centuries and even stronger so during the last decades for both taxonomic groups, and thus, we found no indication that the rate of new establishments slows (Figure 3). This indicates that the pool of potential new invaders has not yet been depleted and that more amphibian and reptile species can be expected to establish in the future. This is in accordance with trends of first records observed for many other taxonomic groups including vascular plants, birds, insects, molluscs, crustaceans and algae (Seebens et al., 2017). Invasions by alien amphibians and reptiles are a rapidly increasing phenomenon, particularly on islands with heterogeneous climates of economically highly developed countries. Our assessment of the global state of these invasions provides the foundation for a future more explicit consideration of these taxonomic groups and relevant pathways in invasion ecology.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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