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

César Capinha¹²,³*  |  Hanno Seebens⁴,⁵*  |  Phillip Cassey⁶  |  Pablo García-Díaz⁶,⁷  |  Bernd Lenzner⁴  |  Thomas Mang⁴  |  Dietmar Moser⁴  |  Petr Pyšek⁸,⁹,¹⁰  |  Dennis Rödder²  |  Riccardo Scalera¹¹  |  Marten Winter¹²  |  Stefan Dullinger⁴  |  Franz Essl⁴,¹⁰*  

¹CIBIO/InBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, Cátedra Infraestruturas de Portugal-Biodiversidade, Universidade do Porto, Vairão, Portugal  
²Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany  
³Global Health and Tropical Medicine (GHTM), Instituto de Higiene e Medicina Tropical (IHMT), Universidade Nova de Lisboa (UNL), Lisboa, Portugal  
⁴Division of Conservation Biology, Vegetation and Landscape Ecology, Department of Biodiversity Research, University of Vienna, Vienna, Austria  
⁵Senckenberg Biodiversity and Climate Research Centre (BiK-F), Frankfurt am Main, Germany  
⁶School of Biological Sciences and Centre for Conservation Science and Technology (CCoST), The University of Adelaide, North Terrace, SA, Australia  
⁷Landcare Research New Zealand, Lincoln, New Zealand  
⁸Institute of Botany, Department of Invasion Ecology, The Czech Academy of Sciences, Průhonice, Czech Republic  
⁹Department of Ecology, Faculty of Science, Charles University in Prague, Prague, Czech Republic  
¹⁰Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, Matieland, South Africa  
¹¹IUCN/SSC Invasive Species Specialist Group, Rome, Italy  
¹²German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany

Correspondence  
Franz Essl, Division of Conservation Biology, Vegetation and Landscape Ecology, Department of Biodiversity Research, University of Vienna, Vienna, Austria. Email: franz.essl@univie.ac.at

Funding information  
Portuguese Foundation for Science and Technology (FCT/MCTES), Grant/Award Number: SFRH/BPD/84422/2012 and GHTM–UID/Multi/04413/2013; POPH/FSE (EC); Austrian Research Foundation, Grant/Award Number: I2096-B16; German Research Foundation, Grant/Award Number: SE 1891/2-1; The Czech Academy of Sciences; German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Grant/Award Number: FZT 118; Commonwealth Government of Australia (DET); ARC Discovery, Grant/Award Number: DP140102319; Future Fellowship, Grant/Award Number: FT0991420

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

*These three authors contributed equally to this manuscript.
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 km² for continental regions (median: 118,073 km²) and between about 1,900,000 to 0.03 km² for island regions (median: 703 km²).

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 herpetile 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; Garcia-Díaz, Ross, Woolnough, & Cassey, 2016; Garcia-Díaz et al., 2015; Powell et al., 2011; Soubeiran 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, & Tinoco, 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 Jonnés, 1818); Lygodactylus capensis (Smith, 1849); Pachydactylus bibronii Bouleneger 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 hermanni 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 TDWG level 4 and of the GADM database of Global Administrative Areas (http://www.gadm.org/) for the countries not included in TDWG 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 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 Herp 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 Herp 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...
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.
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)].

### 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.

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; Jechke & 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,
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 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 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 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 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 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 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 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 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 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 species; c. 11% of extant species).
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.

ACKNOWLEDGEMENTS

Several colleagues have contributed their expertise during the compilation and curation of the data set (in brackets: region for which data have been provided): Marine Arakelyan (Armenia), Luciano Ávila (Argentina), Federico Bolaños (Costa Rica), Luis Ceriaco (Angola), Indraneili Das (India), Mark Hutchinson and Nick Clemm (Australia), José Jesus (Madeira), Petros Lymberakis (Greece); Ulrich Manthey (Indonesia), Dion Maple, Brendan Tiemann and Samantha Flakus (Christmas Island, Australia), Fernando Martínez Freiría and José C. Brito (Western Sahara), James McCranie (Honduras), Ray Pierce (Tokelau), Robert Powell (Caribbean), Jíří Šmíd (Iran), Javier Sunyer (Nicaragua), Aitor Valdeón (Qatar), Harold Voris (Thailand), George Zugh (Pitcairn Islands). CC acknowledges support from the Portuguese Foundation for Science and Technology (FCT/MCTES) and POPH/FSE (EC) (SRH/BPD/84422/2012 and GHTM—UID/Multi/04413/2013). HS, BL, TM, DM, SD and FE and HS acknowledge support by the Austrian Research Foundation (FWF, grant I2086-B16) and by the German Research Foundation (DFG, grant SE 1891/2-1), which also supported DR (grant RO 4520/3-1). PP was supported by long-term research development project RVO 67985939 and Praemium Academiae award (both from The Czech Academy of Sciences). MW acknowledges funding by the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig (DFG FZT 118). PG-D was funded by an IPRS/APA scholarship by the Commonwealth Government of Australia (DET), and an Invasive Animals CRC PhD scholarship. PC was supported by an ARC Discovery Grant (DP140102319) and Future Fellowship (FT0991420). We appreciate the helpful comments by three anonymous referees that contributed to improve the manuscript.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

REFERENCES


---

**BIOSKETCHES**

César Capinha is an ecologist and biogeographer interested in documenting large-scale biogeographical patterns of alien species and in forecasting how these patterns may progress under global change.

Hanno Seebens is an invasion ecologist with interests in the global distribution and spread of alien species, using data analysis and modelling.

Franz Essl is an ecologist with a focus on invasion ecology, macroecology and conservation biology.

**Author Contributions:** CC, FE and HS designed the study. CC, FE, HS, PGD, RS and BL compiled the species data, and DM and BL compiled the explanatory variables. CC and HS analysed the data, with the help of TM and DM. FE, CC and HS led paper writing. All authors further discussed the results and commented on the manuscript.

**SUPPORTING INFORMATION**

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

**How to cite this article:** Capinha C, Seebens H, Cassey P, et al. Diversity, biogeography and the global flows of alien amphibians and reptiles. *Divers Distrib.* 2017;23:1313–1322. [https://doi.org/10.1111/ddi.12617](https://doi.org/10.1111/ddi.12617)