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Global assessment of establishment success for amphibian and reptile invaders

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Abstract

Context. According to the tens rule, 10% of introduced species establish themselves.

Aims. We tested this component of the tens rule for amphibians and reptiles globally, in Europe and North America, where data are presumably of good quality, and on islands *versus* continents. We also tested whether there was a taxonomic difference in establishment success between amphibians and reptiles.

Methods. We examined data comprising 206 successful and 165 failed introduction records for 161 species of amphibians to 55 locations, and 560 successful and 641 failed introduction records for 469 species of reptiles to 116 locations around the world.

Key results. Globally, establishment success was not different between amphibians (67%) and reptiles (62%). Both means were well above the 10% value predicted by the tens rule. In Europe and North America, establishment success was lower, although still higher than 10%. For reptiles, establishment success was higher on islands than on continents. Our results question the tens rule and do not show taxonomic differences in establishment success.

Implications. Similar to studies on other taxa (birds and mammals), we found that establishment success was generally above 40%. This suggests that we should focus management on reducing the number of herptile species introduced because both reptiles and amphibians have a high likelihood of establishing. As data collection on invasions continue, testing establishment success in light of other factors, including propagule pressure, climate matching and taxonomic classifications, may provide additional insight into which species are most likely to establish in particular areas.

Additional keywords: exotic species, herpetofauna, introduced species, invasive species, non-natives, tens rule.

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Introduction

Despite invasion ecology being a complex science, scientists have tried to impart some predictability into the process. One of the first such efforts was the tens rule (Williamson and Brown 1986). Developed for British plants, arthropods and vertebrates, the rule predicts that ~10% of the species introduced to an area establish, and of those, ~10% spread. The rule is based on the idea that there are probabilistic aspects to invasion that should yield some predictability, and the rule has been tested as a benchmark to compare various taxa (Richardson and Pyšek 2006).

Despite the supposed general applicability of the tens rule, it is recognised that different organisms exhibit different probabilities of establishment and spread (Richardson and Pyšek 2006). Furthermore, most tests produce values above 10% (Jeschke and Strayer 2005). For example, Jeschke and Strayer (2005) studied introductions of birds, fish and mammals between Europe and North America and found that establishment and spread ranged from 30% to 85%. Forsyth and Duncan (2001) studied bird and ungulate introductions to New Zealand and found that 34% and 79% established, respectively. Jeschke (2008) conducted a global assessment for birds and mammals and found that 50% and 79% established, and 34% and 63% spread, respectively. There have been previous tests of establishment success for herpetofauna (Kraus 2003, 2009; Bomford *et al*. 2009); however, these studies did not compare amphibian and reptile establishment separately.

Testing the tens rule is not trivial, and it can be difficult to attain data unbiased enough to test the hypothesis. One of the primary concerns with testing the tens rule is the inherent biases in most datasets for successfully introduced rather than failed species that often go unrecorded (Rodriguez-Cabal *et al*. 2009; Sol *et al*. 2008). If data are more complete for successfully introduced than unsuccessful species, establishment success will be positively biased. One way to address this potential issue is to test the rule for areas where data are more complete for both successfully and unsuccessfully introduced species, such as Europe and North America (Jeschke 2009; Kraus 2009).

With the development of a global, comprehensive database of introduced amphibians and reptiles (Kraus 2009), we can now

test for taxonomic differences between amphibians and reptiles in the establishment component of the tens rule (data were not available to address spread). The goals of the present study were (1) to compare establishment success between amphibians and reptiles globally, and compare their success with the tens rule, (2) to test the tens rule against data from only Europe and North America, because these locations presumably have more complete data (Jeschke 2009; Kraus 2009) and (3) to test the hypothesis that islands are more invasible than continents (the island-susceptibility hypothesis; Elton 1958; Simberloff 1995; Jeschke 2008).

Materials and methods

The majority of data used in our analyses were gathered from a database provided by Kraus (2009). This database is the result of an extensive review of the literature on amphibian and reptile introductions globally and has been used in other studies (Bomford *et al*. 2009; Tingley *et al*. 2010, 2011; Poessel *et al*. in press). The data we used from the database included the name of the introduced species, the locality in which the species was introduced (usually a country, but for the United States and Canada, the state or province), and whether or not the introduction was successful (i.e. whether the species became established). The determination of whether a species became successfully established was based on the most recent information available in the literature (i.e. if a species was established for a period of time in a locality but later disappeared, then that introduction was classified as unsuccessful). In addition to the data provided by Kraus (2009), the area of each location was included and each location was designated as belonging to Europe or North America and as island or continent, as appropriate.

To calculate establishment success for amphibians and reptiles, we divided the number of successfully established species by the total number of introduced species, both successful and unsuccessful, for each location in the database. Therefore, our sample sizes reflect the number of locations for which there were data. This differed from a measure of establishment success determined for amphibians and reptiles simultaneously that investigated the number of successfully established species to any location divided by the total number of locations (Bomford *et al*. 2009). Our analysis also differs from those conducted in Kraus (2003, 2009), which are more thoroughly described in the discussion.

To create our final dataset, we modified the database as follows. If a data-entry location reported less than three introduced species, it was deleted because of low confidence in this information (similar to Jeschke 2008). In addition, data for countries that exist on the same island (i.e. Dominican Republic and Haiti) were combined for the analysis.

We examined data comprising 206 successful and 165 failed establishment records for 161 species of amphibians to 55 locations, and 560 successful and 641 failed establishment records for 469 species of reptiles to 116 locations around the world. For a separate, independent analysis, any locations in which either amphibians or reptiles were not introduced were excluded. This step was taken to compare the two taxa using a paired dataset restricted to those locations where data were available for both taxa, which ensured that differences in establishment success were not caused by differences among the locations and reduced the number of locations to 48.

To determine establishment success in areas where data on unsuccessful establishment was likely to be better (Jeschke and Strayer 2005; Rodriguez-Cabal *et al*. 2009), a separate dataset was constructed that included only European and North American locations, and establishment success of amphibians and reptiles was compared between these two regions. Finally, to test the hypothesis that islands are more invasible than continents, we compared establishment success on islands and continents for amphibians and reptiles separately.

Because the Kraus database (Kraus 2009) has more information on some species than others, we also re-ran all statistical analyses excluding the top three most frequently introduced amphibian species (*Lithobates* (*Rana*) *catesbeiana*, *Eleutherodactylus johnstonei* and *Rhinella* (*Bufo*) *marinus*) and reptile species (*Hemidactylus frenatus*, *Ramphotyphlops braminus* and *Trachemys scripta*) from the database.

We used a Wilcoxon rank-sum test to assess differences in establishment success between amphibians and reptiles globally, for Europe and North America, as well as for islands and continents. We used a Wilcoxon signed-rank test to compare establishment success between amphibians and reptiles in areas where both taxa were introduced and to compare establishment success for each taxon with the expected 10% from the tens rule. All values presented are means ±1 standard error. All statistical analyses were conducted in SAS v. 9.3 for Windows (SAS Institute, Cary, North Carolina, USA).

Results

Globally, establishment success was not different between amphibians (67% ± 3.9%, $n = 55$) and reptiles (62% ± 3.1%, $n = 116$) ($T = 4936.5$, $P = 0.489$). Both means were well above the 10% value predicted by the tens rule ($T = 769.0$, $P < 0.001$; $T = 3273.0$, $P < 0.001$, respectively).

When only locations where both amphibians and reptiles were introduced were included, establishment success for amphibians (65% ± 4.2%, $n = 48$) was slightly higher than that for reptiles (55% ± 5.1%, $n = 48$) ($T = 141.0$, $P = 0.048$), and both means were well above the 10% value predicted by the tens rule ($T = 659.0$, $P < 0.001$; $T = 607.0$, $P < 0.001$, respectively).

When only European and North American locations were included, establishment success for amphibians (60% ± 5.7%, $n = 27$) was not significantly different from that for reptiles (45% ± 4.8%, $n = 51$) ($T = 1244.5$, $P = 0.061$) (Fig. 1). Again, both means were well above 10% ($T = 188.0$, $P < 0.001$; $T = 573.5$, $P < 0.001$). When we parsed these data further, establishment success did not differ between amphibians and reptiles in Europe ($T = 196.0$, $P = 0.420$) or North America ($T = 457.5$, $P = 0.097$).

Amphibian establishment success was not different between Europe (58% ± 9.1%, $n = 11$) and North America (62% ± 7.5%, $n = 16$) ($T = 150.5$, $P = 0.882$). Likewise, reptile establishment success was not different between Europe (47% ± 7.9%, $n = 20$) and North America (43% ± 6.3%, $n = 31$) ($T = 543.0$, $P = 0.663$).

Amphibian establishment success was not different between continents (64% ± 5.6%, $n = 27$) and islands (71% ± 5.3%, $n = 28$) ($T = 704.5$, $P = 0.385$) (Fig. 2). Reptile establishment

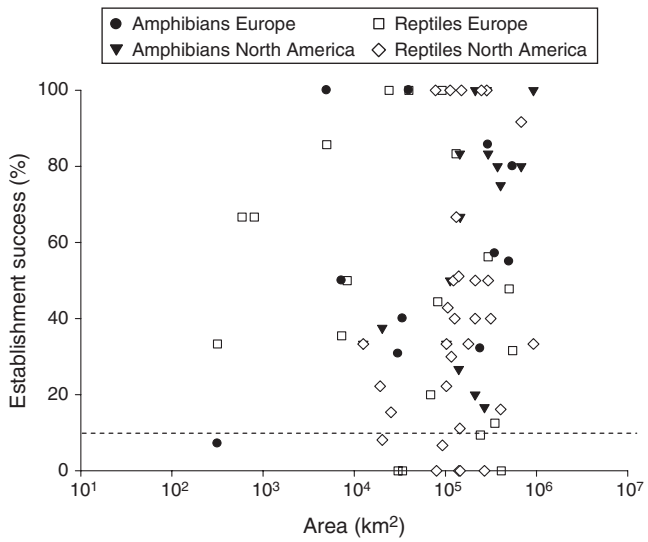

Fig. 1. Establishment success (%) of amphibians in Europe ($n = 11$) and North America ($n = 16$), and reptiles in Europe ($n = 20$) and North America ($n = 31$), and the area of locations (log-transformed) to which the taxa were introduced. Area was used on the *x*-axis to make the plot comparable with Jeschke (2008). The dashed line represents establishment success predicted by the tens rule.

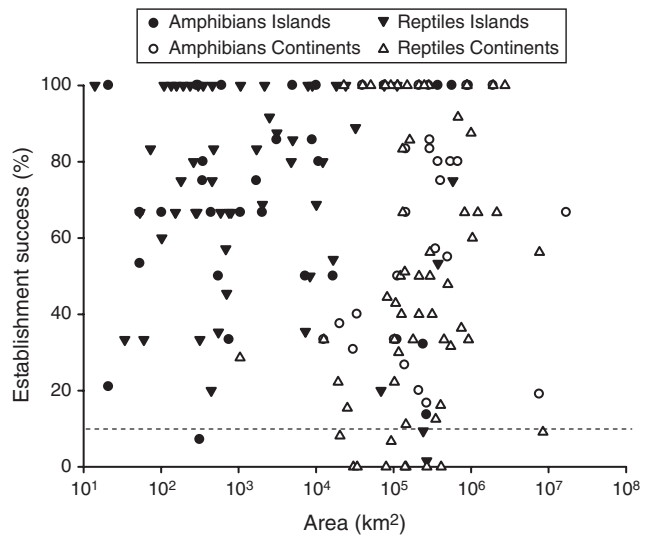

Fig. 2. Establishment success (%) of amphibians on islands ($n = 28$) and continents ($n = 27$), and reptiles on islands ($n = 54$) and continents ($n = 62$) and the area of locations (log-transformed) to which the taxa were introduced. Area was used on the *x*-axis to make the plot comparable with Jeschke (2008). The dashed line represents establishment success predicted by the tens rule.

success was higher on islands (72% ± 3.7%, $n = 54$) than on continents (53% ± 4.6%, $n = 62$) ($T = 3659.5$, $P = 0.005$) (Fig. 2). In all cases, establishment success was well above 10% (for amphibians and reptiles analysed separately on islands and continents: $T > 188.0$, $P < 0.001$).

When we re-ran the statistical analyses without the top three most frequently introduced amphibians and reptiles, there was only one difference in the statistical outcomes of the above described tests. When only locations where both amphibians and reptiles were introduced were included, establishment success for amphibians (59% ± 5.2%, $n = 48$) was no longer higher than that for reptiles (53% ± 5.4%, $n = 48$) ($T = 95.0$, $P = 0.188$).

Discussion

We found no significant difference in establishment success between amphibians and reptiles at a global scale. This was the case whether we investigated all locations invaded by either amphibians or reptiles, or only locations in Europe and North America. The only exception to this was a marginally higher rate of establishment for amphibians in the dataset that included only locations invaded by both amphibians and reptiles; however, this result was no longer significant when the three most frequently introduced amphibians and reptiles were removed from the database. This result differs from those of other studies that have found highly significant taxonomic differences in establishment success, e.g. higher establishment success of mammals than birds globally (Jeschke 2008) and higher establishment success of ungulates than birds in New Zealand (Forsyth and Duncan 2001).

All estimates of establishment success in the present study were between 40% and 70%, which is in the range of estimates from other studies (summarised in Jeschke and Strayer 2005). Establishment success of both taxonomic classes globally, and on islands and continents, far exceeded the 10% value predicted by the tens rule. Even when we investigated only Europe and North America, which are likely to have more complete data on unsuccessful species (Jeschke and Strayer 2005; Jeschke 2009), establishment success was significantly greater than 10%. There are always concerns with the variable 'percentage successfully established species' because it can be positively biased by the lack of data on the number of unsuccessfully established; in addition, all such studies are only as good as the database used. However, because our values consistently were so much higher than 10%, we feel confident that the results suggest that both taxa have a high likelihood of establishing.

There have been previous tests of the tens rule with amphibians and reptiles taken together and by taxonomic order (Kraus 2003, 2009). Kraus (2003) analysed the data by taxonomic order and on herpetofauna together; however, the analyses were conducted with an earlier version of the database; therefore, we focus on results from Kraus (2009). In Kraus (2009), the number of successfully established species (counted only once per location) was divided by the total number of attempted introductions across locations (which may include multiple attempts for the same species). He found that 'percentages of introductions resulting in successful establishment' were 12%, 47% and 18% for continents, large islands and small islands (<6000 km^2), respectively, and <10% and <20% for Europe and North America, respectively (Kraus 2009). Our analysis and the analyses of Kraus both had the number of successfully established species in the numerator. However, analyses of Kraus differed from ours in that our denominator was species scale (unsuccessful plus successful for a location) and his denominator was global scale (total attempted introductions across locations, which may

include multiple introductions for one species), and this would be expected to result in lower percentages.

Bomford *et al.* (2009) explored a similar question at the species level and calculated establishment success as the number of locations successfully invaded by a species divided by the total number of locations where the species had been introduced. Bomford *et al.* (2009) found that 52% of herptiles established globally, using this calculation. Even though all of these studies used the same database (Kraus 2009), our results differed because the analyses differed. We believe our analysis is more comparable to others asking similar questions regarding differences in establishment success between taxa (Forsyth and Duncan 2001; Jeschke 2008). In addition, we looked at amphibians and reptiles independently to compare them, and this has not been done previously.

We found that reptile establishment success was significantly higher on islands than on continents, supporting the hypothesis that islands are more susceptible to invasion by reptiles than are continents (Elton 1958; Simberloff 1995); however, this was not the case for amphibians. Kraus (2003, 2009) found support for this hypothesis for herptiles in general; however, as described above, our analyses differed. Our result also differed from those in Tingley *et al.* (2011), who found support for the island-susceptibility hypothesis for amphibians. Tingley *et al.*'s (2011) 'predicted probability of establishment' for amphibians on continents and islands were ~70% and 75%, respectively, and, therefore, slightly higher than our values of 64% and 71%, respectively. The difference might be attributed to a difference in datasets (we eliminated locations with <3 introductions) as well as different analyses; Tingley *et al.*'s (2011) predicted probabilities of establishment were derived from a minimum adequate model that included taxonomic classifications, biogeographic realm, presence of congeners, climate matching and propagule pressure.

In conclusion, similar to other studies, our results question the tens rule (Kraus 2003, 2009; Jeschke and Strayer 2005; Jeschke 2008; Bomford *et al.* 2009). It appears that establishment success is lower where there are more complete data (i.e. Europe and North America), and thus the difficulty in testing the rule remains. However, it may not simply be that where data are more complete, there are better records of unsuccessful species, and therefore establishment success is lower. It may also be that where records are better, there is also better management of non-natives. In addition, it may become more or less difficult to invade areas where there have been more invasions (Elton 1958; Simberloff and Von Holle 1999). Although we believe that tests of these hypotheses are important for prioritising management, we also appreciate that as data collection on invasions continue, interpreting results of such a simple rule in light of other factors, such as propagule pressure, climate matching and taxonomic classifications, will improve our ability to predict successful establishment.

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