



RESEARCH
PAPER

Biotic acceptance in introduced amphibians and reptiles in Europe and North America

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ABSTRACT

Aim The biotic resistance hypothesis argues that complex plant and animal communities are more resistant to invasion than simpler communities. Conversely, the biotic acceptance hypothesis states that non-native and native species richness are positively related. Most tests of these hypotheses at continental scales, typically conducted on plants, have found support for biotic acceptance. We tested these hypotheses on both amphibians and reptiles across Europe and North America.

Location Continental countries in Europe and states/provinces in North America.

Methods We used multiple linear regression models to determine which factors predicted successful establishment of amphibians and reptiles in Europe and North America, and additional models to determine which factors predicted native species richness.

Results Successful establishment of amphibians and reptiles in Europe and reptiles in North America was positively related to native species richness. We found higher numbers of successful amphibian species in Europe than in North America. Potential evapotranspiration (PET) was positively related to non-native species richness for amphibians and reptiles in Europe and reptiles in North America. PET was also the primary factor determining native species richness for both amphibians and reptiles in Europe and North America.

Main conclusions We found support for the biotic acceptance hypothesis for amphibians and reptiles in Europe and reptiles in North America, suggesting that the presence of native amphibian and reptile species generally indicates good habitat for non-native species. Our data suggest that the greater number of established amphibians per native amphibians in Europe than in North America might be explained by more introductions in Europe or climate-matching of the invaders. Areas with high native species richness should be the focus of control and management efforts, especially considering that non-native species located in areas with a high number of natives can have a large impact on biological diversity.

Keywords

Biotic resistance, herpetofauna, native species richness, non-native species, Northern Hemisphere, potential evapotranspiration.

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INTRODUCTION

The introduction and spread of non-native species is one of the most important threats to biological diversity (Wilcove *et al.*,

1998) and is responsible for severe impacts on ecological systems and human health (Elton, 1958; Kraus, 2009). Understanding the factors that influence the success of non-native species is critical. Such factors may include taxonomic or demographic

characteristics of invaders and ecological features of invaded communities (Richardson & Pyšek, 2006). The association between native species diversity and the successful establishment of non-native species has been studied extensively (e.g. Stohlgren *et al.*, 1999; Levine, 2000; Naem *et al.*, 2000), but questions regarding the diversity–invasibility relationship still remain.

Elton (1958) argued that simple plant and animal communities were more vulnerable to invasions than more complex communities (i.e. the biotic resistance hypothesis) because the balance of relatively simple communities can be more easily disturbed and more subject to population fluctuations than richer communities. However, many plant studies have shown a positive relationship between native and non-native species richness at large spatial scales (e.g. Stohlgren *et al.*, 1999; Sax, 2002). This relationship is so pervasive it has been referred to as the biotic acceptance hypothesis (Stohlgren *et al.*, 2006). One likely mechanism for this pattern is that both native and non-native plants respond similarly to a group of environmental factors, e.g. available resources (Stohlgren *et al.*, 2003; Gilbert & Lechowicz, 2005). The relationship between native and non-native species richness for animal taxa is less well known. Negative relationships have been found at small scales with marine invertebrates (Stachowicz *et al.*, 1999) and reptiles on islands (Case & Bolger, 1991), whereas positive relationships have been shown at larger scales with invertebrates (Burger *et al.*, 2001) and mammals (Jeschke & Genovesi, 2011). These differing results illustrate that patterns of successful establishment of non-native species may not be consistent for animal taxa, although positive relationships appear to be favoured at large spatial scales.

Several variables can influence the success of non-native species and are believed to be of importance when testing the biotic resistance hypothesis. These include: (1) area, because of the well-known species–area relationship (Rosenzweig, 1995); (2) human population size, because of the higher numbers of some non-native species where human density is greater (McKinney, 2006); (3) number of introductions, because of its important role in the variation of non-native species richness (Lonsdale, 1999); and (4) climate, such as potential evapotranspiration (PET), which has been shown to explain a large amount of the variability in species richness (Currie, 1991; Rodríguez *et al.*, 2005; Whitton *et al.*, 2012). While area, human population size and climate are relatively easy to measure, data on number of introductions are often not available.

In addition, many factors influence the occurrence of native species in a particular locality. These include, but are not limited to: (1) area, again because of the species–area relationship (Rosenzweig, 1995); (2) climate, again because it explains variability in species richness (Currie, 1991; Rodríguez *et al.*, 2005; Whitton *et al.*, 2012); and (3) elevation, e.g. the distribution of native species diversity along altitudinal gradients (Lomolino, 2001). If native species richness is related to the success of non-native species, then understanding the factors that have the strongest effects on native species might assist in the management of non-native species.

Numerous studies have analysed introductions of non-native plants, birds and mammals (e.g. Moulton & Pimm, 1983; Tilman, 1997; White & King, 2006), but fewer have examined non-native amphibians and reptiles. Bomford *et al.* (2009) determined that the number of introduction events for non-native amphibians and reptiles was correlated with successful establishment, and that successful species had better climate matches between their native and introduced ranges than failed species. Similarly, van Wilgen & Richardson (2012) found that propagule pressure was the variable most strongly associated with amphibian and reptile establishment success. Tingley *et al.* (2011) demonstrated that establishment success of amphibians was higher when congeneric species were present at introduction locations, and that pre-adaptation played an important role in their establishment success. In contrast, van Wilgen & Richardson (2011) found that successfully established reptile species were more distantly related to native species than introduced reptiles that failed to establish. Case & Bolger (1991) determined that reptile communities on islands with high native diversity were more resistant to the invasion of introduced reptiles than island communities with low native diversity, supporting the biotic resistance hypothesis. This hypothesis, however, has not yet been tested with amphibians or reptiles at continental scales.

Because data on species introductions can be poor in some areas (Sol *et al.*, 2008), tests of the diversity–invasibility relationship should be conducted in regions with well-documented information on introduced species and whether they successfully established. Europe and North America are two such regions that have been well studied and where high-quality records are available for introductions (Jeschke & Strayer, 2005; Kraus, 2009). The objectives of our study were to determine: (1) which of five variables were related to successful amphibian and reptile establishment in continental areas in Europe and North America; and (2) which of three variables were related to native amphibian and reptile species richness in continental areas in Europe and North America.

METHODS

Data collection

We obtained data on amphibian and reptile introductions from a global database provided by Kraus (2009) that represents a majority of herpetological introductions that have occurred throughout the world. The database included records for frogs, toads, salamanders, lizards, snakes, turtles and crocodiles. The data we used from the database consisted of 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), whether or not the introduced species became successfully established, and the number of independent introductions of that species to that locality. 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.

ful. We obtained additional data for each locality to supplement the database, including annual PET (mm), area (km²), minimum and maximum elevation (m) and average human population size, as well as the number of native amphibians obtained from the International Union for Conservation of Nature Red List of Threatened Species (<http://www.iucnredlist.org/>) and the number of native reptiles obtained from The Reptile Database (<http://www.reptile-database.org>). We chose PET as our climate predictor because this variable has previously been found to explain a majority of the variance in terrestrial vertebrate species richness in North America (Currie, 1991) and reptile species richness in Europe (Rodríguez *et al.*, 2005). PET data were obtained from the Consortium for Spatial Information (Trabucco & Zomer, 2009). Area data were obtained from NationMaster for European countries (http://www.nationmaster.com/graph/geo_are_lan-geography-area-land; accessed 7 March 2011), StateMaster for states (http://www.statemaster.com/graph/geo_lan_are-geography-land-area; accessed 7 March 2011), and Natural Resources Canada for provinces (<http://atlas.nrcan.gc.ca/site/english/learningresources/facts/surfareas.html>; accessed 7 March 2011). Elevation data were obtained from NationMaster for European countries (http://www.nationmaster.com/graph/geo_ele_ext_low_poi-geography-elevation-extremes-lowest-point and http://www.nationmaster.com/graph/geo_ele_ext_hig_poi-geography-elevation-extremes-highest-point; accessed 9 March 2011), the United States Geological Survey for states (<http://egsc.usgs.gov/isb/pubs/booklets/elvadist/elvadist.html#Highest>; accessed 9 March 2011) and Natural Resources Canada for provinces (<http://atlas.nrcan.gc.ca/site/english/learningresources/facts/faq.html#points>; accessed 9 March 2011). Human population data were obtained from the Socioeconomic Data and Applications Center for European countries (<http://sedac.ciesin.columbia.edu/gpw/>; accessed 16 March 2011), the United States Census Bureau for states (<http://www.census.gov/compendia/statab/2011/ranks/rank01.html>; accessed 16 March 2011) and Statistics Canada for provinces (<http://www.statcan.gc.ca/tables-tableaux/sum-som/l01/cst01/demo02a-eng.htm>; accessed 16 March 2011) for the years 2000–10. We focused our analyses on continental locations: countries within Europe, states within the United States and provinces within Canada.

With these data we created four different datasets: (1) amphibian introductions in Europe; (2) amphibian introductions in North America; (3) reptile introductions in Europe; and (4) reptile introductions in North America (Fig. 1; Appendix S1 in Supporting Information). We only included locations in each region where amphibian introductions or reptile introductions occurred. The mean area for all locations included in each region was $178,998 \pm 175,793$ SD (km²) for Europe and $214,379 \pm 259,843$ SD (km²) for North America. Total native species richness across study locations in Europe and North America was 77 and 270 for amphibians, and 125 and 294 for reptiles, respectively. Total successfully established non-native species richness across study locations in Europe and North America was 25 and 28 for amphibians, and 24 and 68 for reptiles, respectively.

Data analysis

We used multiple linear regression models to determine which factors predicted successful establishment of non-native amphibians and reptiles in Europe and North America. The response variable was number of successfully established species. We did not use percentage of successfully established species as the response because the number of unsuccessful species was not readily available in the Kraus (2009) database. Predictor variables included: (1) native species richness; (2) area; (3) human density (calculated as human population size per km²); (4) number of introductions, i.e. release events; and (5) PET. The number of introductions variable was included in our models at the location level (the level of our analyses), rather than at the species level, to represent introduction pressure at a specific location. Because the number of successfully established species might be dependent on the number of introductions, we first corrected the number of introductions by subtracting the number of successfully established species in each location (Lockwood *et al.*, 2009). However, model results were not substantially different; hence, we used the uncorrected number of introductions as a predictor in all models. In addition, we corrected native species richness for area, following Jeschke & Genovesi (2011) and Lonsdale (1999), by calculating residuals from a regression of natives on area. However, the number of native species was not significantly correlated with area for any region or taxon (Europe amphibians $r = 0.53$, $P = 0.094$; North America amphibians $r = -0.23$, $P = 0.128$; Europe reptiles $r = 0.47$, $P = 0.069$; North America reptiles $r = 0.20$, $P = 0.187$). In addition, native species richness was still a significant predictor of successful amphibians and reptiles in Europe and successful reptiles in North America, even after correcting natives for area (Appendix S2). Hence, we used the raw variable of native species richness as a predictor in all models.

We first ran four multiple linear regression models, one for each taxon in each region for those locations that had introduction data, with native species richness, area, human density and number of introductions as predictor variables. For each model, we transformed the response variable when appropriate to meet distributional assumptions, and we used backward selection to choose the most appropriate model and eliminate multicollinearity, with a significance level to stay in the model of 0.05. We tested for outliers in the data and determined that, for the successful establishment of reptiles in North America, Florida had a high number of successes (46). However, these data were accurate, the successful establishment of species was real, and the results of the model did not change with Florida removed. Hence, we could not justify eliminating Florida as an outlier (Stohlgren *et al.*, 2003). Next, we ran four additional models with successfully established species as the response (transformed when appropriate) and PET as the only predictor. We did not include PET as a predictor in our original models with successfully established species as the response variable because of the high correlation between native species and PET. Such correlation results in the elimination of one of the correlated variables by model selection, and our objective was to test the

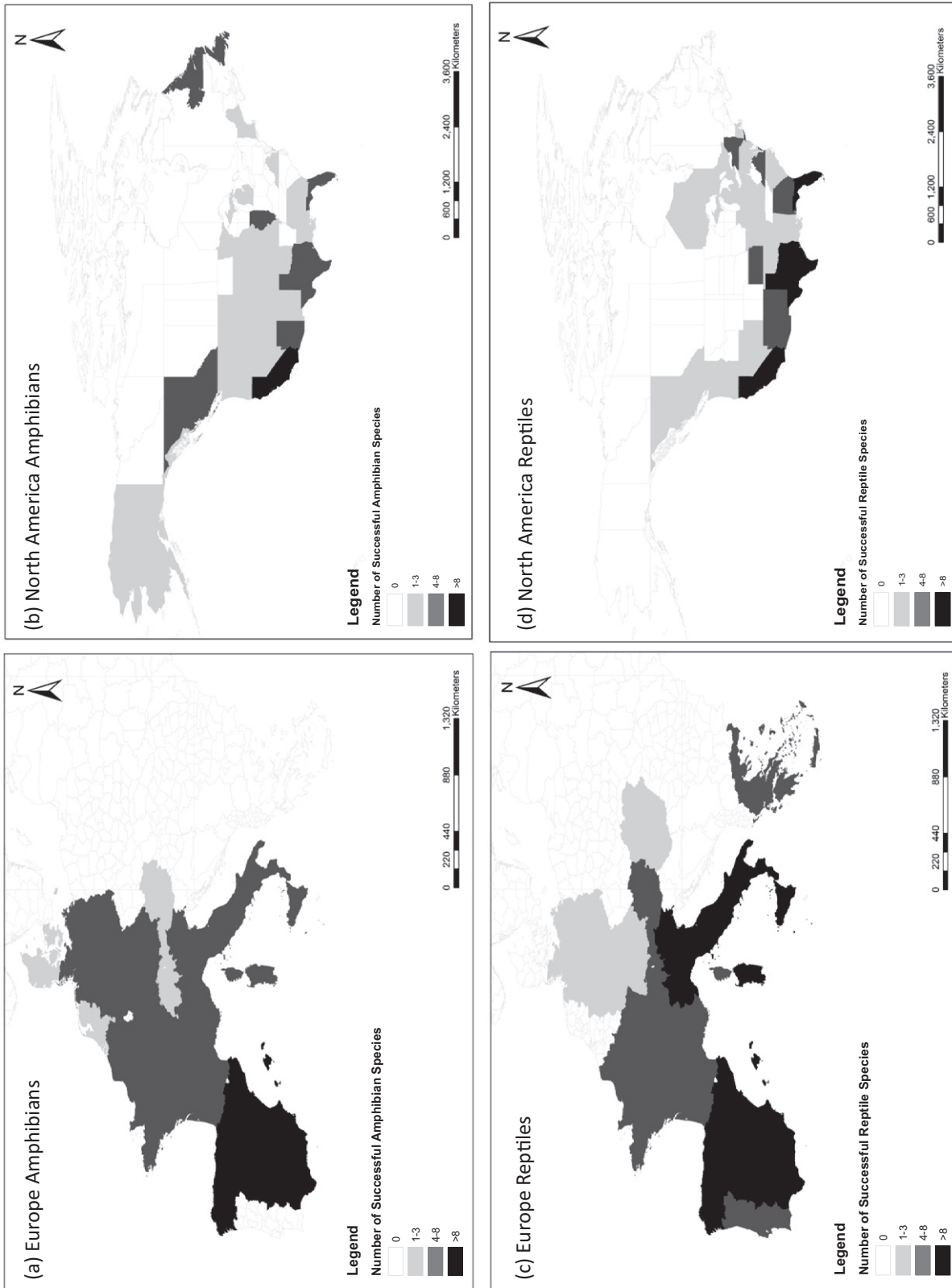


Figure 1 Map of numbers of successfully established species for (a) amphibians in Europe, (b) amphibians in North America, (c) reptiles in Europe and (d) reptiles in North America according to Kraus (2009). Zero values indicate that either no introduced species successfully established in that location or that no introductions occurred in the Kraus (2009) database. Data are presented at the country level for Europe and at the state/province level for North America. The map projection is Geographic Coordinate System WGS 1984.

effect of native species richness on successfully established species. Finally, we ran an additional model for each taxon and region for those locations that had introduction data with native species richness as the response (transformed when appropriate) and area, PET and range in elevation (difference between maximum and minimum elevation) as predictors to determine which environmental factors affected the numbers of native species.

Because we found a difference in the diversity–invasibility relationship between Europe and North America (see Discussion), we ran two generalized linear models, one for amphibians and one for reptiles, with successfully established species as the response variable, region (Europe or North America) as a factor and native species richness and number of introductions as covariates. We tested the interaction between native species richness and region to determine if the difference we observed in the relationship between successfully established and native species between the two regions was significant. All statistical analyses were conducted in SAS v.9.2 (SAS Institute Inc., 2008).

RESULTS

For non-native amphibians in Europe, native species richness and number of introductions were important predictors of successful establishment ($F_{2,8} = 17.68$, $P = 0.001$; Table 1). Both predictors were positively related to successfully established species (native species richness, Fig. 2a; introductions, Fig. 3a).

PET was positively related to successfully established species ($F_{1,9} = 13.17$, $P = 0.006$; Table 1, Appendix S3a). PET was the only significant predictor of native amphibians ($F_{1,9} = 23.45$, $P = 0.001$; Table 1) and was positively related to native species richness (Appendix S3b).

For non-native amphibians in North America, area and number of introductions were important predictors of successful establishment ($F_{2,41} = 44.31$, $P < 0.001$; Table 1). Both predictors were positively related to successfully established species (area, $R^2 = 0.07$; introductions, Fig. 3a). Native species richness was not related to successfully established species (Fig. 2a). PET also was not related to successfully established species ($F_{1,42} = 1.69$, $P = 0.201$; Table 1, Appendix S3a). PET was the only significant predictor of native amphibians ($F_{1,42} = 64.49$, $P < 0.001$; Table 1) and was positively related to native species richness (Appendix S3b). The relationship between successfully established and native amphibians was different between Europe and North America ($\chi^2 = 41.47$, $P < 0.001$).

For non-native reptiles in Europe, native species richness was the only important predictor of successful establishment ($F_{1,14} = 10.67$, $P = 0.006$; Table 1) and was positively related to successfully established species (Fig. 2b). Number of introductions was not a significant predictor of successfully established species (Fig. 3b). PET was positively related to successfully established species ($F_{1,14} = 9.11$, $P = 0.009$; Table 1, Appendix S3c). PET and area were both significant predictors of native reptiles ($F_{2,13} = 18.23$, $P < 0.001$; Table 1) and were positively related to native species richness (PET, Appendix S3d; area, $R^2 = 0.22$).

Table 1 Model selection results for European and North American amphibians and reptiles.

Model	Region	Taxon	Significant predictors	Parameter estimate	P-value	R ² of model	n
1	Europe	Amphibians	Native species richness	0.056	0.001	0.82	11
			No. of introductions	0.019	0.034		
2	Europe	Amphibians	PET	0.004	0.006	0.59	11
3	Europe	Amphibians	PET	0.060	0.001	0.72	11
1	North America	Amphibians	Area	< 0.001	0.023	0.68	44
			No. of introductions	0.107	< 0.001		
2	North America	Amphibians	NS	n.a.	n.a.	0.04	44
3	North America	Amphibians	PET	0.001	< 0.001	0.61	44
1	Europe	Reptiles	Native species richness	0.015	0.006	0.43	16
2	Europe	Reptiles	PET	0.001	0.009	0.39	16
3	Europe	Reptiles	PET	0.076	< 0.001	0.74	16
			Area	< 0.001	0.044		
1	North America	Reptiles	Native species richness	0.003	0.001	0.64	46
			No. of introductions	0.003	< 0.001		
2	North America	Reptiles	PET	0.001	< 0.001	0.28	46
3	North America	Reptiles	PET	0.149	< 0.001	0.73	46
			Area	< 0.001	< 0.001		

Three models were run for each region/taxon combination, two for successfully established species and one for native species. One model for successfully established species included native species richness, area, human density and number of introductions as predictor variables (coded as 1); the second model included annual potential evapotranspiration (PET) as the only predictor variable (coded as 2). The model for native species included area, PET and range in elevation as predictor variables (coded as 3).

Significant predictor variables ($P < 0.05$) for each model are shown.

n = sample size for each model. NS, no significant predictor variables; n.a., not applicable.

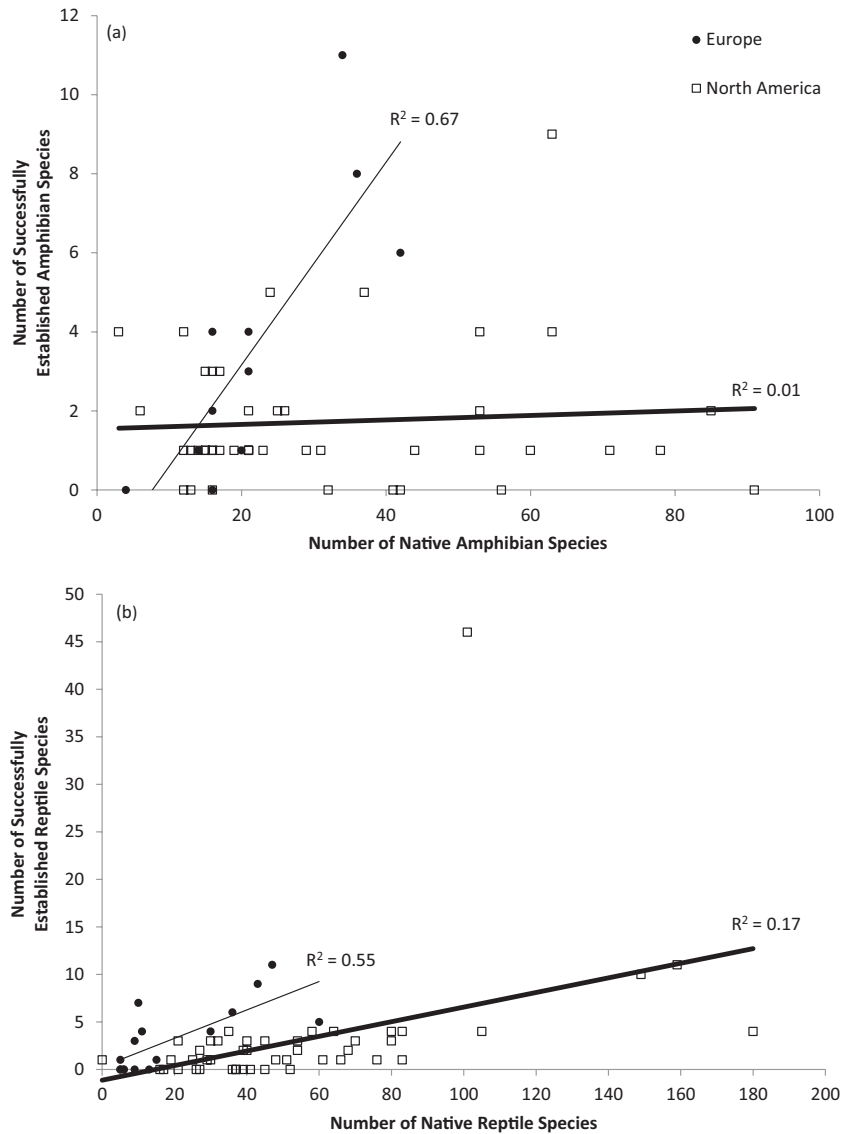


Figure 2 Scatterplots of relationship between (a) successfully established amphibian species and native amphibian species and (b) successfully established reptile species and native reptile species in Europe and North America. The thin line represents the trend line for Europe; the thick line represents the trend line for North America. $n = 11$ for amphibians in Europe, 44 for amphibians in North America, 16 for reptiles in Europe and 46 for reptiles in North America.

For non-native reptiles in North America, native species richness and number of introductions were important predictors of successful establishment ($F_{2,43} = 38.20, P < 0.001$; Table 1). Both predictors were positively related to successfully established species (native species richness, Fig. 2b; introductions, Fig. 3b). PET was positively related to successfully established species ($F_{1,44} = 16.88, P < 0.001$; Table 1, Appendix S3c). Both PET and area were significant predictors of native reptiles ($F_{2,43} = 59.07, P < 0.001$; Table 1) and were positively related to native species richness (PET, Appendix S3d; area, $R^2 = 0.04$). The relationship between successfully established and native reptiles was not different between Europe and North America ($\chi^2 = 0.42, P = 0.519$).

DISCUSSION

We found a positive relationship between successfully established amphibians and reptiles in Europe and reptiles in North America and native species richness, even after accounting for

other potentially important variables. We also determined that PET was a significant predictor of successfully established amphibians and reptiles in Europe and reptiles in North America, the same taxa and regions where native species richness predicted successful establishment. In addition, we found that PET was the primary factor determining native species richness for both amphibians and reptiles in both Europe and North America. For reptiles, area was also important for native species richness in both regions, a result that was not unexpected due to the species–area relationship. However, area was not an important predictor of native amphibian richness.

Based on available data and the predictors that we used, we determined that the biotic acceptance hypothesis (Stohlgren *et al.*, 2006; Jeschke & Genovesi, 2011) was supported for amphibians and reptiles in Europe and for reptiles in North America. Our results suggest that native amphibian and reptile species do not competitively exclude non-natives from successfully establishing at continental scales, in contrast to Case &

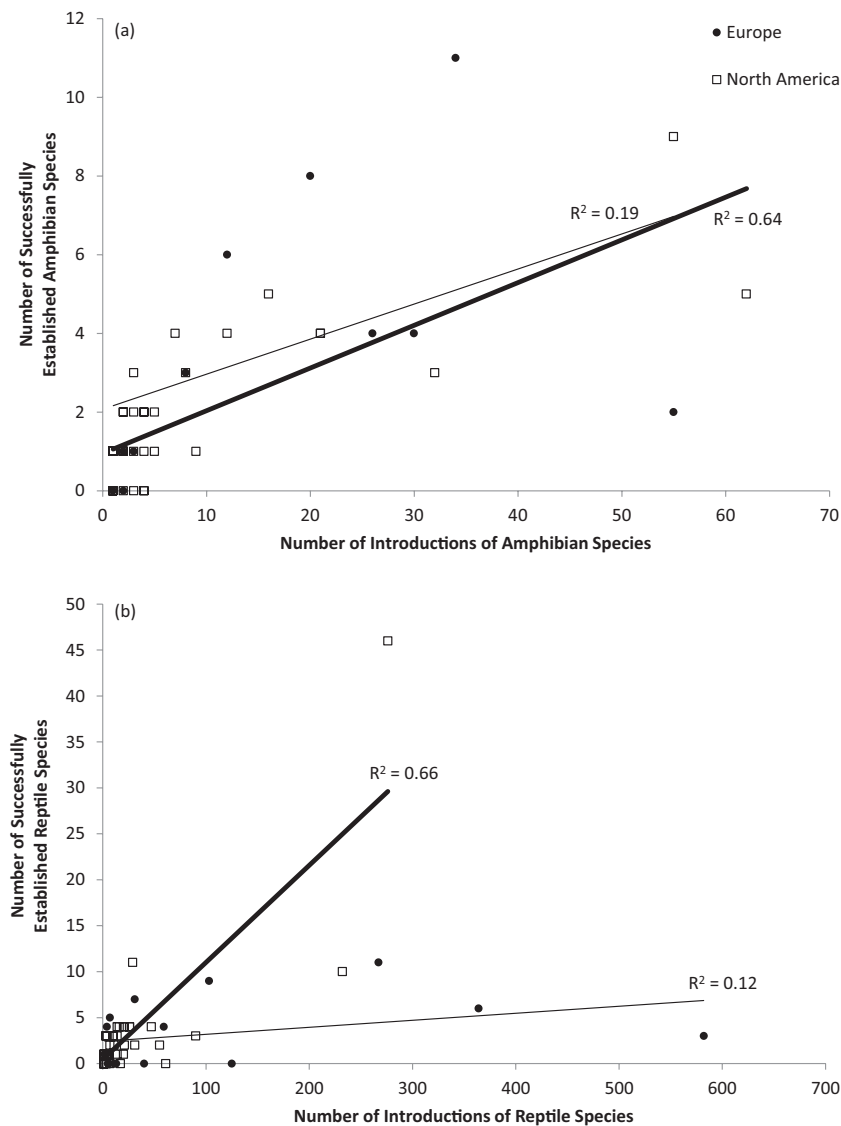


Figure 3 Scatterplots of relationship between (a) successfully established amphibian species and number of introductions and (b) successfully established reptile species and number of introductions in Europe and North America. The thin line represents the trend line for Europe; the thick line represents the trend line for North America. $n = 11$ for amphibians in Europe, 44 for amphibians in North America, 16 for reptiles in Europe and 46 for reptiles in North America.

Bolger (1991) for reptiles on islands, but rather that native species richness generally indicates good habitat for non-native species. PET appears to drive the relationship between native and non-native species, providing further support that both natives and non-natives respond similarly to environmental gradients (Stohlgren *et al.*, 2006). PET was included as a predictor in our models to describe climatic variation in latitudinal space, based on previous findings on climate–richness relationships for these taxa in these regions. Currie (1991) determined that PET explained more than 90% of the variability in terrestrial vertebrate species richness in North America, Rodríguez *et al.* (2005) found that PET explained 71% of the variance in reptile species richness in Europe and Whitton *et al.* (2012) found that PET was an important factor in determining global geographic ranges of amphibians. Perhaps area was not a significant predictor of native amphibian species richness because amphibians are known to be more limited by specific habitat types than by area (Becker *et al.*, 2010).

An alternative explanation for our results indicating a positive relationship between successfully established and native species is that facilitation among reptiles and amphibians may be driving this pattern. However, at our scale of analysis, findings are unlikely to incorporate direct interactions between native and non-native species, e.g. predation, competition or facilitation (Pearson & Dawson, 2003; Bisrat *et al.*, 2012). At smaller scales, species are more likely to interact and biotic resistance may be more likely to occur. To our knowledge, this study is the first to determine biotic acceptance in amphibian and reptile species at continental scales.

The only exception to our results for successfully established species was the outcome of the model for amphibians in North America, which demonstrated no relationship between native and non-native species (Fig. 2a) and no relationship between PET and non-native species. Several hypotheses might explain these patterns. First, while we might expect biotic resistance to be more important at smaller scales (and it does not appear to be

driving the general patterns observed in this study) some level of biotic resistance could be occurring in North America for amphibians, i.e. biotic resistance might be reducing the effect of a positive relationship between native and non-native amphibian species (Fig. 2a). Second, efforts at controlling non-native amphibian species in North America might be responsible for their low numbers even where native species richness is high. Kraus (2009) discussed successful eradication of African clawed frogs (*Xenopus laevis*) in the United States; however, many other efforts to control non-native amphibians have not been successful [e.g. bullfrogs (*Rana catesbeiana*) in Arizona; Kraus 2009]. Finally, the state/province scale might not be the most appropriate scale to use for this analysis; however, we found a strong positive relationship between native amphibians and PET at this scale (Appendix S3b), so the scale argument does not seem relevant.

Europe had more successfully established amphibian species than North America when native species richness was equal (Fig. 2a). Several possible factors might explain this pattern. First, European countries had a greater mean number of amphibian introductions than did North American states/provinces (Europe, 18 ± 5 SE; North America, 7 ± 2 SE; Fig. 3a). Because North America has not yet had as many introductions of amphibians as Europe, the number of successfully established species in North America may not be as high as in Europe but may increase in the future as introductions continue to increase. Thus, current differences between these two regions may be reduced over time. Second, Europe just may be easier to invade than North America. Habitats in Europe may be more disturbed, improving the success of non-native species (Rodda & Tyrrell, 2008), or they may be less saturated than in North America, an assumption that is not unreasonable because the herpetological biota is richer in North America than in Europe (see Methods; Jeschke & Strayer, 2005; Buckley & Jetz, 2007). Ecosystems in Europe may be able to withstand a greater number of amphibian species than the number of native species that currently reside there, allowing non-native species to successfully establish. Third, the difference between Europe and North America could be a function of the types of species that have been introduced to each region. The percentage of successful amphibian species in Europe that were native to Europe (50%) was higher than the percentage of successful amphibian species in North America that were native to North America (34%). Perhaps the higher success rate in Europe than in North America was a consequence of more non-native species in Europe that originated from other parts of the same continent in similar latitudinal bands and climates (i.e. climate matching). Finally, control and management efforts of non-native amphibian species may not be as heavily emphasized in Europe as in North America, allowing more non-native species to establish or become successful in Europe. Genovesi (2005) reported a total of 37 eradication programmes successfully completed in Europe to 2002; most of these involved non-native rodents and none included amphibians, although Kraus (2009) discussed bullfrog eradications in England and Germany.

In conclusion, the successful establishment of non-native species was positively related to native species richness, suggesting that biotic acceptance occurs for amphibians and reptiles in Europe and for reptiles in North America. PET predicted successful establishment of the same taxa and regions where native species richness predicted successful establishment. PET was the primary factor affecting native species richness, while area was also important to native reptiles. The management and conservation implications of these findings are that areas with high native species richness indicate good habitat for non-native species, and these areas should be the focus of control and management efforts, especially considering that non-native species located in areas with a high number of natives can have a great impact on biological diversity. Although the relationship between native species and successful non-native species is often positive for many taxa at regional scales, our results for amphibians suggest that the shape of this relationship may differ between regions. Simply acknowledging the existence of biotic acceptance for a particular taxon may no longer be sufficient. Differences in the relationship between regions are worth considering when determining the most effective management and conservation strategies to avoid establishment of non-native species.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Data used in linear regression models.

Appendix S2 Results of linear regression models where native species richness is corrected for area.

Appendix S3 Scatterplots of relationships between successfully established/native species and annual potential evapotranspiration in Europe and North America.

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BIOSKETCH

The research team was brought together by a shared interest in non-native amphibian and reptile species and global patterns in the successful establishment of such species.

Author contributions: S.P. collected data, did the analyses and led the writing. K.B. conceived the ideas, collected data and provided valuable comments. C.C., R.F. and E.S. collected data and provided valuable comments.

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