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Predicting establishment success for alien reptiles and amphibians: a role for climate matching

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Abstract We examined data comprising 1,028 successful and 967 failed introduction records for 596 species of alien reptiles and amphibians around the world to test for factors influencing establishment success. We found significant variations between families and between genera. The number of jurisdictions where a species was introduced was a significant predictor of the probability the species had established in at least one jurisdiction. All species that had been introduced to more than 10 jurisdictions (34 species) had established at least one alien population. We also conducted more detailed quantitative comparisons for successful (69 species) and failed (116 species) introductions to three jurisdictions (Great Britain, California and Florida) to test for associations with climate match, geographic range size, and history of establishment success elsewhere. Relative to failed species, successful species had better climate matches between the jurisdiction where they were introduced and their geographic range elsewhere in the world. Successful species were also more likely to have high establishment success rates elsewhere in the world. Cross-validations indicated our full model correctly categorized establishment success with 78–80% accuracy. Our findings may guide risk assessments for the import of live alien reptiles and amphibians to reduce the rate new species establish in the wild.

Keywords Alien species · Amphibians · Climate matching · Establishment success · Prediction · Reptiles · Risk assessment

Abbreviations

ROC	Receiver operating characteristic curve
USA	United States of America

Introduction

Alien species are transported via a variety of pathways (Carlton et al. 2003), with pathway importance varying taxonomically. Once alien species are admitted to a new country there is no such thing as zero risk of escape or release (Shine et al. 2000). Six pathways have been identified as of primary importance in the spread of alien reptiles and amphibians, but these show significant temporal, taxonomic, and geographic variation (Kraus 2003). The pet trade, deliberate introductions for personal aesthetic pleasure, cargo hitch-hikers, and nursery-trade hitch-hikers have been especially important in the dispersal

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of alien herpetofauna in recent decades. Deliberate or accidental release of pets and aquarium specimens is an especially serious problem.

Alien species in new environments can cause major economic damage and irreversible ecological changes (Pimentel et al. 2000; Pimentel 2002; Bomford 2003; Andersen et al. 2004). Impacts documented for alien reptiles and amphibians include, for example, extinctions or declines of native prey species (Fritts and Rodda 1998; Karube and Suda 2004; Greenlees et al. 2006), poisoning of native predators (Doody et al. 2006a, b, competitive displacement (Boland 2004; Cole et al. 2005), disease transmission (Daszak et al. 1999; Garner et al. 2006), hybridization with and genetic swamping of native species (Arntzen and Thorpe 1999; Riley et al. 2003; Storfer et al. 2004), evolutionary changes in native species (Phillips and Shine 2004, 2006a, b), economic damage (Fritts et al. 1987; Fritts and McCoid 1999; Fritts and Chiszar 1999; Kaiser and Burnett 2006), and human-health damage (Fritts et al. 1990, 1994). Many additional examples exist (Kraus in preparation), yet impacts from invasive herpetofauna have been little studied.

While improved public education about the risks posed by alien species may reduce the incidence of releases, it is also desirable to restrict the import and keeping of high-risk species (Reed 2005). To achieve this goal, risk assessments are needed to identify which species are most likely to establish.

Government legislation in some countries (e.g., New Zealand) now requires that the risk that imported alien species might establish wild pest populations be assessed before import is permitted. In theory, science-based risk assessments of alien species' invasive potential can enable quarantine authorities to permit the import of low-risk species, whilst identifying and excluding high-risk species (Kolar and Lodge 2002; Bomford 2003). This will maintain trade and enable alien species to be imported for productive and recreational uses, whilst protecting against potential pest species (Keller et al. 2007). Yet how such risks can be assessed is still a matter for debate, and some ecologists consider that generalisations across taxonomic groups are not feasible (Williamson 1999; Kolar and Lodge 2001; Heger and Trepl 2003; Cassey et al. 2004). Risk assessments need to be accurate, open, and repeatable in order to minimise risk. There is a pressing need to formulate scientifically sound methods and approaches in the field of risk assessment for invasive species (Andersen et al. 2004). Ecologists continue to suggest and test a large number of attributes in search of a set that is consistently associated with establishment success, and risk analysts continue to recommend their use in risk-management schemes (Kolar and Lodge 2002; Stohlgren and Schnase 2006; Hayes and Barry 2008).

Hayes and Barry (2008) examine 24 studies that identified correlates of establishment success across six animal groups and find only three characteristics are consistently associated with establishment success across taxa: climate/habitat match, establishment success elsewhere, and propagule pressure (number of arriving/released individuals and/or number of release events). Hayes and Barry (2008) conclude that risk managers can place faith in risk assessments based on these factors, while warning that results must be interpreted carefully. Information on the last two factors will frequently be unavailable for reptiles or amphibians, leaving climate match most broadly reliable.

We found no previously published studies on factors affecting the introduction success of alien reptiles or amphibians. We examined data for published introduction records worldwide to see if number of introduction events or taxonomic group are correlated with establishment success. We also examined records of introduction outcomes for reptiles and amphibians introduced to Great Britain, California and Florida to test for associations between establishment success and climate match between the jurisdiction where they were introduced and their geographic range elsewhere in the world, and their history of establishment success elsewhere in the world.

A key component of our analyses was climate matching between origin and release sites based on rainfall and temperature data. A 'climate envelope' approach was used in which a species' world geographic range (including both its native and introduced ranges but excluding the jurisdiction being tested) was mapped and the climatic attributes measured, and then locations with matching climate attributes were determined for the jurisdiction being tested. Climate matching can be used to generate maps of establishment likelihood for a species from any part of the world to a nominated target region (Pheloung 1996; Sutherst et al. 1998; Baker et al.

2000; Duncan et al. 2001; Kriticos and Randall 2001; Forsyth et al. 2004).

Methods

Introduction data

Data comprised literature records for 596 species introduced around the world; of these, there were records for 1,028 successful establishments and 967 failed introductions. These data were taken from a global database of alien herpetological introductions that will be published in an updated form in its entirety (Kraus in preparation). This sample represents a large majority of the world's published instances of introductions involving reptiles and amphibians. We classified species as either established or failed for each jurisdiction to which it was introduced—a jurisdiction being either a country or, for North America, a state or province. Many records consisted of multiple introductions of the same species to the same jurisdiction, but a successful establishment indicates only that at least one of these was successful; it was impossible to determine from the literature the fate of each instance of introduction. Further, assessments of success or failure were based on the most recent information in the literature. Species introductions that persisted for several decades but eventually died out were categorized as failures. We excluded records from our analyses if identification to species was uncertain, or the outcome of the introduction (established or failed) was unknown or uncertain. Most introductions in the database were intentional movements via the pet trade, followed by accidental imports in cargo shipments.

We chose a subset of the data comprising 175 records for Great Britain, Florida, and California (Table 1) to test the importance of climate matching in determining establishment success. These three jurisdictions were selected because they each had a reasonable sample of both successful and failed species representing a wide taxonomic range and because the CLIMATE data base contained a reasonable number of meteorological stations spread across each jurisdiction. For Florida, only alien species introduced from outside the USA were included. For California, species translocated from the eastern states of the USA were included to increase the sample size, but translocated species native to California were excluded. For Britain, only species introduced from outside the British Isles were included. World range data included both native and alien ranges but excluded the range in the target jurisdiction (Britain, California or Florida); these were sourced from literature and web databases for each species and digitized.

Table 1 Numbers of alien reptile and amphibian species introduced to Britain, California and Florida

Jurisdiction	Successful	Failed	Total
Britain	12	39	51
California	13	49	62
Florida	47	33	80

Climate matching

We used a climate-matching procedure to quantify the climatically suitable habitat available to each introduced species within the three target jurisdictions. For a species introduced to Britain, for example, the climate match between Britain and the species' world geographic range outside Britain (including any introduced range) was calculated using CLIMATE (Bureau of Rural Sciences 2006). The CLIMATE software contains data for 16 temperature and rainfall variables (Table 2) imported from BIOCLIM (Busby 1991) for 8,331 meteorological stations worldwide (in the worlddata_all.txt climate data source file). CLIMATE calculates a climate-match score for each meteorological station within Britain based on the minimum Euclidian distance in the 16-dimensional variable space between that meteorological station and all other world meteorological stations in the species' geographic range outside Britain. Each variable is normalised by dividing it by its worldwide standard deviation. These climate-match scores range from 10 for the highest level match to zero for the poorest match. For a meteorological station in Britain to have scored highly, it must have matched closely all 16 climatic variables of at least one meteorological station in the species' geographic range outside Britain. When assessing a species' climate match to Britain we summed the number of meteorological stations with climate-match scores at each level. We then calculated cumulative scores, i.e., for each match level we summed the number of meteorological

Table 2 The 16 climate parameters used to estimate the extent of climatically matched habitat in the CLIMATE program

Temperature parameters (°C)	Rainfall parameters (mm)
Mean annual	Mean annual
Minimum of coolest month	Mean of wettest month
Maximum of warmest month	Mean of driest month
Average range	Mean monthly coefficient of variation
Mean of coolest quarter	Mean of coolest quarter
Mean of warmest quarter	Mean of warmest quarter
Mean of wettest quarter	Mean of wettest quarter
Mean of driest quarter	Mean of warmest quarter

Estimates of these parameters are derived from long-term averages of monthly minimum and maximum temperatures and rainfall for each of the 8,331 meteorological stations in the CLIMATE database

stations with scores at that level and at all higher match levels to create Sum Climate scores. For example, Sum Climate 8 includes data for climate match scores in the three highest match levels (8, 9 and 10) whereas Sum Climate 5 also includes lower match levels (5–10). We then expressed these Sum Climate scores as percentages of the total number of meteorological stations in Britain to enable us to make comparisons with other jurisdictions. We used the same process to calculate Sum Climate% scores for the species introduced to Florida and California. We then repeated the climate-matching analyses twice, restricting our analyses to either the eight temperature variables or the eight rainfall variables in Table 2.

World range size

We plotted each species' world geographic range, excluding the species' range within the recipient jurisdiction being assessed, onto a world map traced with five-degree (latitude by longitude) grid squares. We then counted the number of occupied grid squares in each latitude band to the nearest 0.1 of a grid square. We used a spreadsheet to convert the number of occupied grid squares in each latitude band to an equivalent number of square kilometres and summed these values to obtain the total world range size.

Phylogenetic factors

Correction for phylogenetic non-independence is a common approach in assessing factors correlated with establishment success or invasiveness (Sol and Lefebvre 2000; Forsyth et al. 2004). Statistically, this approach is necessary if we believe that we have a taxonomically non-random sample compared to the population for which we wish to make inference (biased sampling).

The use of generalized linear mixed models with phylogenetic group as a random effect(s) would appear to be the most natural statistical way of incorporating this variation (Wood 2006). In our generalised linear mixed model we had:

$$\mathrm{Logit}(\Pr(\mathrm{invasive})) = \mathrm{X}b + r \tag{1}$$

where r is the random effect which has mean zero and variance σ^2 and represents systematic variation between taxonomic groups unexplained by the co-variates, X is a matrix of co-variates, and b are the regression parameters. This conditioned out the effect of taxonomy, which corrected for any bias in b caused by the biased taxonomic sampling. For prediction, we used our estimate of r if the taxon has been observed before. Otherwise, we incorporated our fitted value of σ^2 into the prediction.

Higher-level relationships among reptiles and amphibians have undergone considerable revision and controversy in recent years, with family definitions often changing considerably. For amphibians we followed the family-level taxonomy of Frost et al. (2006). For squamates and crocodilians we followed Zug et al. (2001) updated for Gekkota according to Han et al. (2004) and for Serpentes according to Slowinski and Lawson (2002) and Lawson et al. (2005). For turtles we followed Gaffney and Meylan (1988) updated for Geoemydidae according to Spinks et al. (2004).

Analyses

We tested whether species, genus, family or order were correlated with establishment success for the

1995 introduction records of alien reptiles and amphibians around the world. We calculated each species' introduction success rate as the number of jurisdictions where the species was successfully introduced divided by the total number of jurisdictions where the species was introduced. We calculated genus success rate as the number of times species in that genus were successfully introduced to any jurisdiction divided by the total number of times species in that genus were introduced to any jurisdiction. We repeated this process for family, order and class. We used these taxon-success rates to rank 596 species, 266 genera, 46 families, and five orders according to their establishment-success rates. We analysed these data using a generalised linear mixed model where we partitioned the variation between the three levels: order, family, and genus. We modelled probability of successful introduction, p, as:

$$\mathrm{Logit}(P) = \mathrm{alpha} + \mathrm{order} + \mathrm{family} + \mathrm{genus} \tag{2}$$

where alpha is the intercept and order, family and genus are Gaussian random effects with mean zero and separate variances. These partitioned the variations for each level.

We tested the significance of the number of jurisdictions where a species has been introduced on the probability of successful introduction in at least one location, q, as:

$$\begin{aligned}\mathrm{Logit}(q) = {} & \mathrm{alpha} + \mathrm{order} + \mathrm{family} + \mathrm{genus} \\ & + \log(\text{number of jurisdictions})\end{aligned} \tag{3}$$

where log (number of jurisdictions) is a fixed effect and alpha, order, family and genus are as in the previous model. We transformed the number of jurisdictions to the logarithmic scale to create a linear relationship.

We also conducted quantitative comparisons for 175 species introduced to three jurisdictions (Great Britain, California, and Florida) to test for associations with climate match, global geographic range size, and history of establishment success elsewhere.

Statistical arguments suggest it is better to model variables jointly rather than one at a time, as this allows the analysis to consider the effects of confounding variables and provides more concise results with a clearer interpretation. Our data were analysed by a generalised additive mixed model (Wood 2006). This model is an extension of generalised additive models (Hastie and Tibshirani 1990). We modelled the probability of successful introduction, p, as:

$$\begin{aligned}\mathrm{Logit}(p) = {} & s(\mathrm{climate}) + \mathrm{jurisdiction} \\ & + \mathrm{prop.success.species} \\ & + \mathrm{prop.success.genus} \\ & + \mathrm{prop.success.family} + \mathrm{familyre}.\end{aligned} \tag{4}$$

In this model, s(climate) is a smooth function of the climate match score expressed as a proportion of all data locations in the jurisdiction, jurisdiction allows the mean prevalence in countries to vary, and the prop. * variables denote the proportion of introductions at each taxonomic level that were successful worldwide. Familyre is a family random effect assumed drawn from a Gaussian distribution with mean zero and variance that is estimated from the data. Although reptile and amphibian phylogenies are not well resolved, Familyre accounts for systematic variation in invasion success between genera and attempts to quantify the unexplained variation between genera after the known characteristics of the species are taken into account. To fit this as a fixed effect was not statistically defensible because the number of additional parameters needed would be prohibitively large. A smooth function was used for the climate match to allow for the fact that there may not be a linear relationship between the raw sum of Climate and probability of establishment. The smooth function allows the relationship to vary. A smooth term was not considered for all variables because of the number of parameters involved.

To explore the relationship between extent of climate match and probability of invasion success we fitted a model for each level of the climate match and looked for consistency of effects. We note that these variables are strongly correlated, so the results should be interpreted carefully. The model was fit using the statistical package R and the gamma function in the mgcv library.

We used receiver operating characteristic (ROC) curves to determine the range of model predictions likely to indicate species establishment. ROC curves are obtained by plotting the rate of true positives versus false positives based on a range of test thresholds (Lobo et al. 2007). ROC curves are a useful tool to guide selection of a threshold to convert continuous predicted probabilities into binary predictions.

The ability of the fitted model to correctly classify new data was determined using a 10-fold cross-validation approach. This involved partitioning the dataset into 10 subsamples. Of the 10 subsamples, one was used as validation data for testing the model predictions and the remaining nine were used as training data on which the model was fitted. This process was then repeated a further nine times, i.e., using each subsample as the validation dataset. The resulting models were then applied to the test datasets and model predictions compared with observed values, using the threshold determined through the ROC curve analysis.

Results

Global introductions

Of 1995 introduction events of alien reptiles and amphibians to jurisdictions around the world, 51.5% were successful. We found both genus ($P < 2.2 \times 10^{-16}$) and family ($P = 1.54 \times 10^{-9}$) were significant predictors of establishment success. Taxonomic order was marginally significant ($P = 0.089$), with Anura being the most successful order (297 of 482 introductions being successful = 61.6%), followed by Squamata (549/1007 = 54.5%), Caudata (35/80 = 43.8%), Testudines (144/398 = 36.2%) and Crocodilia (3/28 = 10.7%). Species effects were independent, conditional on the higher-level random effects, and most species had patterns of establishment that were indistinguishable from random (Fig. 1). The most and least successful taxa are presented in Table 3.

The number of jurisdictions where a species had been introduced was a significant predictor of the probability of at least one successful introduction ($P < .0001$). All species that had been introduced to more than 10 jurisdictions (34 species) had established an alien population in at least one jurisdiction.

Introductions to Britain, California and Florida

Relative to failed species, successful species had significantly higher climate-match scores in the jurisdiction to which they were introduced (Fig. 2) at all four levels of climate match tested (Table 4). Climate matching using all 16 rainfall and temperature parameters gave better discrimination between successful and failed species than analyses using either the eight temperature (Table 4) or the eight rainfall (Table 4) parameters alone.

Relative to failed species, successful species also had significantly higher establishment success rates in other jurisdictions (Table 4). The jurisdiction where the introduction occurred was also significantly associated with introduction outcome, with Britain having 24% of introduced species establishing, California 21%, and Florida 41%. Geographic range size was not significantly associated with species' establishment success.

We used ROC curves to identify the threshold value corresponding to equal numbers of false negative and false positive establishment outcomes in our full model (Fig. 3). The results of a 10-fold cross-validation based on a threshold of 0.4 for each of the 12 models summarised in Table 4 are listed in Table 5.

Discussion

We used data on successful and failed introductions of alien reptiles and amphibians to test for factors associated with establishment success. For our global data set, we found both genus and family were significant predictors of establishment success. The number of jurisdictions where a species was introduced was also a significant predictor of the probability of there being at least one successful introduction. Our findings support those of Hayes and Barry (2008) who found that number of release events was consistently associated with establishment success in studies on finfish, insects, mammals, and birds. Repeated releases over an extended period increase the chance of successful invasion simply because the release 'experiment' is repeated many times, under different biotic and abiotic conditions, including different climates and seasons, and condition of released animals (Williamson 1999; Kolar and Lodge 2001).

Relative to failures, we found species successfully introduced to Britain, California, and Florida had significantly higher climate-match scores in the recipient jurisdiction and were also significantly more likely to have high establishment success rates elsewhere. In contrast, global geographic range size was not associated with establishment success. The

Table 3 Establishment success residual values estimated by the model (Eq. 2) for alien reptile and amphibian (A) families, (B) genera and (C) species

A.

Most successful families	Residual value	Least successful families	Residual value
Typhlopidae	1.293	Colubridae	−0.622
Gekkonidae	1.188	Viperidae	−0.721
Teiidae	1.015	Salamandridae	−0.880
Proteidae	0.932	Elapidae	−0.974
Agamidae	0.919	Boidae	−1.477

B.

Most successful genera	Residual value	Least successful genera	Residual value
Ramphotyphlops	1.985	*Holbrookia*	−0.610
Trachemys	1.973	*Hymenochirus*	−0.621
Lycodon	1.371	*Ophisaurus*	−0.652
Hemidactylus	1.143	*Python*	−0.668
Triturus	1.129	*Lacerta*	−0.741
Chamaeleo	0.992	*Sceloporus*	−0.742
Lipinia	0.987	*Thamnophis*	−0.744
Hemorrhois	0.965	*Terrapene*	−0.779
Telescopus	0.965	*Gekko*	−0.820
Necturus	0.962	*Uromastyx*	−0.963
Emys	0.955	*Leptodactylus*	−0.993
Calotes	0.947	*Phrynosoma*	−1.115
Eleutherodactylus	0.927	*Egernia*	−1.120
Caiman	0.889	*Lampropeltis*	−1.183
Anolis	0.864	*Gopherus*	−1.261

C.

Most successful species	Residual value	Least successful species	Residual value
Ramphotyphlops braminus	2.328	*Cynops pyrrhogaster*	−0.810
Hemidactylus mabouia	2.202	*Litoria caerulea*	−0.810
Hemidactylus frenatus	1.600	*Malaclemmys terrapin*	−0.810
Rana catesbeiana	1.549	*Micrurus fulvius*	−0.810
Eleutherodactylus johnstonei	1.546	*Python sebae*	−0.810
Hemidactylus turcicus	1.487	*Terrapene ornata*	−0.810
Necturus maculosus	1.486	*Ambystoma mexicanum*	−0.899
Rana perezi	1.486	*Lampropeltis triangulum*	−0.899
Sphaerodactylus argus	1.486	*Macroclemys temminckii*	−0.899
Eleutherodactylus planirostris	1.420	*Natrix natrix*	−0.899
Hemidactylus flaviviridis	1.394	*Gopherus berlandieri*	−0.973
Rana ridibunda	1.361	*Terrapene carolina*	−0.990
Calotes versicolor	1.294	*Lampropeltis getula*	−1.038
Anolis cristatellus	1.282	*Mauremys caspica*	−1.038
Phelsuma dubia	1.282	*Pseudemys floridana*	−1.038
Rana berlandieri	1.282	*Python regius*	−1.038

Table 3 continued

C.

Most successful species	Residual value	Least successful species	Residual value
Varanus indicus	1.282	*Python reticulatus*	−1.038
Lipinia noctua	1.220	*Thamnophis sirtalis*	−1.038
Lepidodactylus lugubris	1.168	*Alligator mississippiensis*	−1.192

All taxa are listed in descending order of establishment success. There were 47 families, 268 genera and 596 species in our database, but only the taxa that were most and least successful at establishing alien populations are presented

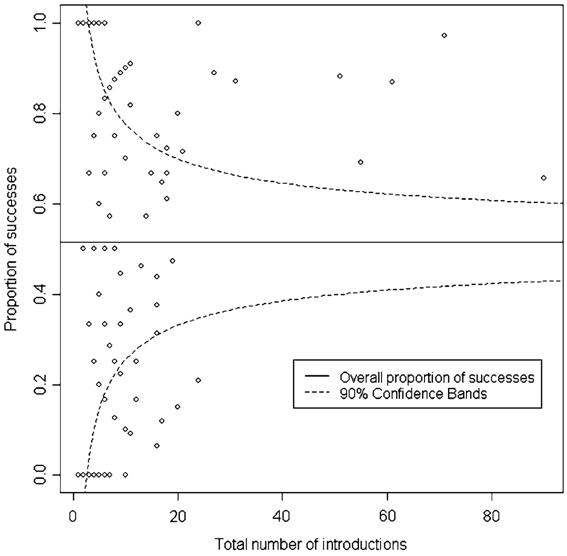

Fig. 1 Proportion of alien reptile and amphibian introductions that resulted in establishment for 1995 introduction events of 596 species. Multiple introductions of the same species into a single jurisdiction are only counted as a single introduction event; hence, the proportion of successes (y-axis) is the number of jurisdictions in which a species is established divided by total number of jurisdictions to which it has been introduced. Lines show the upper and lower 90% confidence bands (smoothed to the outer points of the fitted lines) around the overall proportion established (0.515) based on a binomial distribution. Most species fell within these confidence limits and thus had patterns of establishment that were indistinguishable from random. Species with particularly high and low rates of establishment are presented in Table 3C

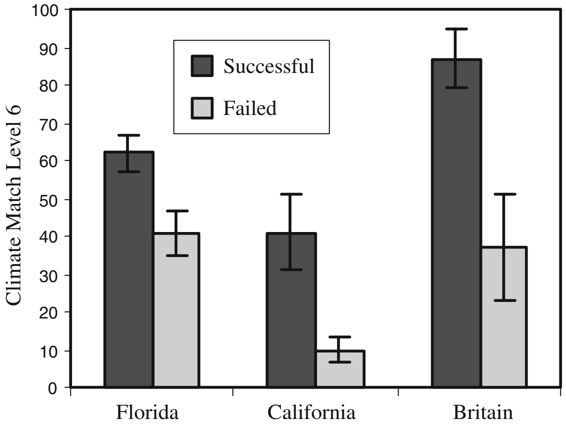

Fig. 2 Average climate-match scores (Sum Climate 6 for 16 climate parameters expressed as a percentage of the total number of meteorological stations in each jurisdiction with standard error bars) for alien reptiles and amphibians introduced to Florida, California, and Britain

results of 10-fold model cross-validation showed our full model correctly classified 78–80% of species.

Several caveats must temper interpretation of our results. First, our data did not represent a random selection of the world's reptile and amphibian species. Many families and most genera have not been introduced anywhere, and our sample was biased towards species from the pet trade or liable to human commensalism. Scientific reporting biases will also over-represent successfully established species (Kraus 2003). Nonetheless, for the sample of taxa known to be introduced by humans, our findings demonstrated that climate match and history of successful establishment elsewhere served as reliable predictors of which introductions were likely to succeed.

Second, we showed that propagule pressure was important in establishment success, but our assessment could only quantify number of recipient jurisdictions and not numbers of released animals or numbers of independent release events because those more detailed data are virtually absent from the literature. Those unavailable data may account for some of our ROC misclassifications. Hayes and Barry (2008) review 10 studies that investigate the relationship between the number of released individuals and establishment success for alien birds and fish, and

Table 4 Statistical probabilities of significance for six factors tested by logistic regression analyses (Eq. 4) for alien reptiles and amphibians introduced to Florida, California, and Britain

Factor	Sum Climate 5	Sum Climate 6	Sum Climate 7	Sum Climate 8
P-values for 16 rainfall and temperature climate parameters				
Jurisdiction	5.79×10^{-6}***	3.93×10^{-5}***	0.000299***	6.38×10^{-6}***
Species success rate	0.00132**	0.00367**	0.020225**	0.00572**
Genus success rate	0.50209	0.46104	0.365586	0.47769
Family success rate	0.13498	0.10750	0.335662	0.23239
World range size	0.15723	0.13671	0.454797	0.53577
Climate match	2.24×10^{-5}***	2.47×10^{-7}***	2.29×10^{-5}***	1.15×10^{-5}***
P-values for the eight temperature climate parameters				
Jurisdiction	0.000391***	0.00313**	0.00876**	0.0161*
Species success rate	0.002282**	0.00686**	0.01200*	0.0341*
Genus success rate	0.993110	0.38742	0.33872	0.3653
Family success rate	0.256629	0.25794	0.28782	0.4184
World range size	0.346213	0.25023	0.28281	0.5649
Climate match	1.18×10^{-5}***	1.34×10^{-5}***	8.23×10^{-6}***	0.000315***
P-values for the eight rainfall climate parameters				
Jurisdiction	0.000124***	0.000102***	5.0×10^{-5}***	1.09×10^{-7}***
Species success rate	0.005466**	0.004448**	0.00320**	0.000101***
Genus success rate	0.925858	0.871957	0.78186	0.141136
Family success rate	0.795478	0.768579	0.57549	0.242423
World range size	0.848189	0.915041	0.42823	0.045236*
Climate match	0.0749	0.0346*	0.00441**	6.72×10^{-8}***

Twelve models were tested: three combinations of climate parameters × four Sum Climate Match levels

* $P < 0{\cdot}05$, ** $P < 0{\cdot}01$, *** $P < 0{\cdot}001$

all the studies demonstrate a significant association. However, species of long-lived reptiles and amphibians that have large clutch or litter sizes and are either parthenogenic or able to store sperm for years may be less dependent on large or multiple introductions to successfully establish wild populations (Reed 2005).

Third, our taxonomic measures of success may have been overly sensitive to taxa introduced only a few times but which were successful by chance (e.g., Proteidae, *Hemorrhois*, *Telescopus*). We give greater credence to results for taxa introduced many times.

Fourth, climate matching set the broad parameters for determining if an area was suitable for a species to establish, but was not a complete explanation because biotic factors, such as the absence of suitable food, nest sites or shelter, or the presence of competitors, predators or diseases, may have excluded species from areas with an otherwise suitable climate. Although a suite of biotic attributes (such as body size, diet, offspring per year, growth rate, lifespan or adaptation to disturbed habitat) has been proposed to influence establishment success for alien vertebrates (Kolar and Lodge 2001, 2002; Reed 2005) none are demonstrated to have consistent effects across taxa (Hayes and Barry 2008). We did not test biotic variables because, for most of the species in our database, we could not obtain sufficient reliable data. However, such analyses may be feasible on a smaller sample of relevant taxa—an assessment beyond the scope of this study. Hence, the importance of biotic attributes in determining establishment success among reptiles and amphibians remains to be determined.

Our findings may prove useful in developing quantitative risk-assessment models that can identify potential invaders and so help governments take preventative action to slow the rate of herpetological invasions. Species with high global introduction success rates (and high propagule pressure) are considered to pose a high risk of establishing in any

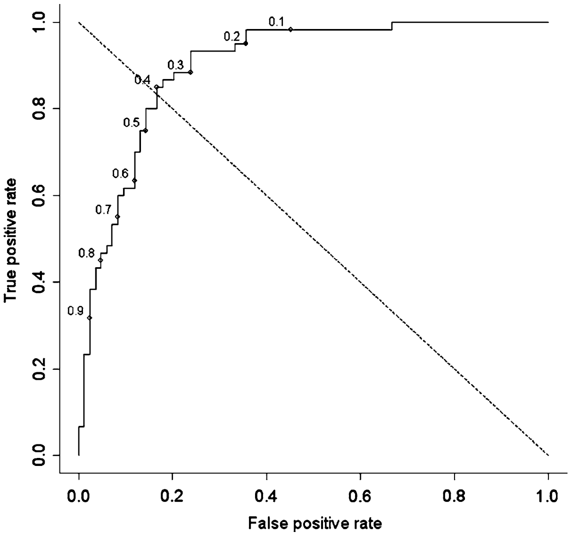

Fig. 3 ROC curve based on the model (Eq. 4) for Sum Climate 6 with 16 climate parameters. The threshold giving equal weighting to false negatives and false positives corresponds to the point where the ROC curve crosses over the diagonal line that runs from the top left point of the plot to the bottom right point of the plot. This was approximately 0.4 for all four levels of climate matching with 16 climate parameters summarised in Table 4, i.e., a model prediction of less than 0.4 indicated a prediction the species would not establish and a prediction of 0.4 or greater predicted the species was likely to establish

Table 5 Results of 10-fold model cross-validation using models based on 16 climate parameters, eight temperature parameters or eight rainfall parameters, indicating the percentage of our species introduction outcomes that were correctly classified (established or failed) by our model (Eq. 4)

Level of climate matching	Sixteen climate parameters (%)	Eight temperature parameters (%)	Eight rainfall parameters (%)
Sum Climate 5	78	78	78
Sum Climate 6	80	77	76
Sum Climate 7	79	80	74
Sum Climate 8	78	80	80

future introductions. Previously unsampled species that come from a genus or family having a high introduction success rate may also pose a high risk, although there is scope for further testing here. Species having a close climate match to the jurisdiction where they are introduced will also pose a high-risk. Species exhibiting risk due to both taxonomic and climate-matching attributes may be expected to pose the highest risk. Establishment success involves complex interactions between the invading species and the physical and biological characteristics of the recipient environment, which may be case-specific and include positive feedback mechanisms (Noble 1989), Allee effects (Drake 2004), and genetic variability (Holdgate 1986). To cope with these complexities it may be desirable to use a combination of qualitative and quantitative methods to provide a framework for risk assessments for alien species introductions (Sikder et al. 2006; Stohlgren and Schnase 2006). Sikder et al. (2006) suggest that this combination approach is required, as quantitative data alone are insufficient to deal with the complexities and uncertainties inherent in invasive species' interactions with their environment.

We used ROC curves to determine the range of model predictions likely to indicate species establishment. We chose a threshold value that gave equal numbers of false negative and false positive outcomes. For risk-assessment modelling, a different threshold could be selected if a higher or lower establishment risk was required. Our fitted model could be used to classify new species data to estimate establishment risk for species introduced to the three jurisdictions used in our study. Extending our findings to develop quantitative assessment models for other jurisdictions will require additional work because we found jurisdiction was significantly correlated with establishment success in our models, and the cause of this variation is as yet uncertain.

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