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Distance to native niche margins explains establishment success of alien mammals

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Abstract

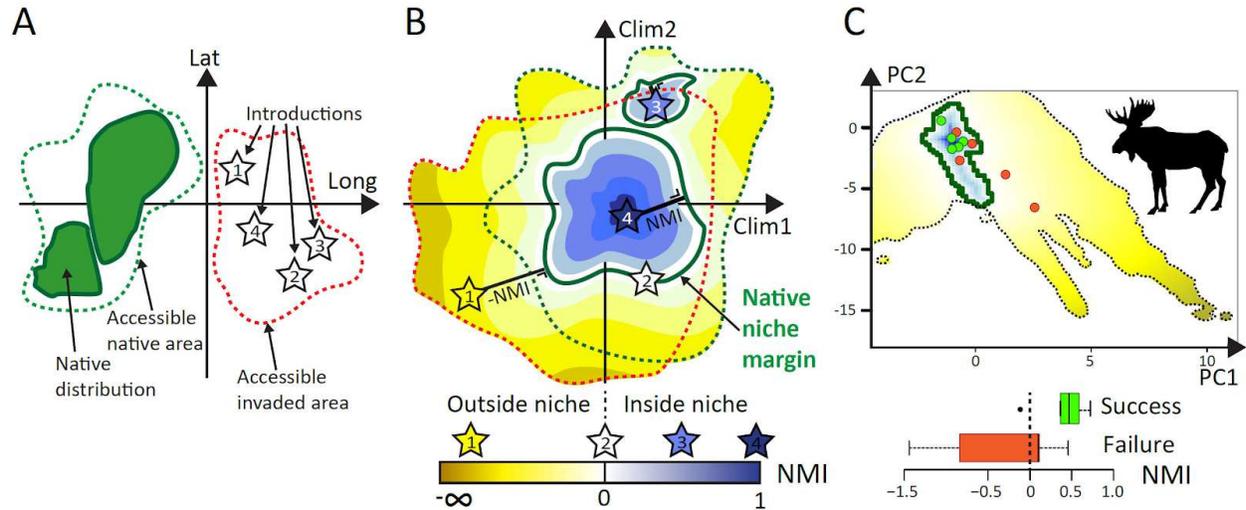
Why do some alien species introductions fail while others are successful? One key hypothesis is that in order for a species to invade a new range, it must initially establish successfully in conditions within its native climatic niche (NCN). Yet, this hypothesis has largely remained untested at the level of individual release events. Using a dataset of 989 introductions of 177 mammal species worldwide, we show that climatic matching to the NCN, measured by a new Niche Margin Index (*NMI*), is a stronger predictor of establishment success than most previously tested life-history attributes and historical factors. Contrary to traditional climatic suitability metrics derived from species distribution models, the *NMI* is based on niche margins and provides a measure of how distant a site is inside or, importantly, outside the NCN. Integrating *NMI* as a measure of NCN-matching in risk assessments could improve efforts to prevent invasions and avoid costly eradications.

Investigating the factors responsible for the establishment success of alien species is crucial for understanding the proximate drivers of species invasions (1) and for designing management tools (2). To establish in a new territory, a species must successfully pass through a series of filters (3): it must be translocated there, find suitable abiotic conditions to grow and reproduce, and withstand the new biotic settings in the invaded community. The abiotic environment is a critical filter, often considered through the prism of the species' environmental niche (4). A pressing question in this regard is whether an introduction is more successful if it occurs at a site where the climatic conditions belong to the ensemble of conditions experienced by the species within its native range (i.e. the native climatic niche, NCN). A traditional assumption is that the closer a site is to the NCN center, the greater the chances of successful establishment (5). However, because niches are often asymmetrical (6), the NCN center does not necessarily describe an ecological optimum (7). In such instances the distance to NCN margins should be a better descriptor of how suitable a site is for establishment (6), because population fitness is expected to decrease toward margins (4). Surprisingly, although many studies have revealed that niche shifts can occur between the native and invaded ranges of alien species (8) none has investigated whether establishment can take place outside the NCN. So far, the importance of NCN-matching for establishment has remained largely untested, and no studies used distance from NCN margins.

We identify four main reasons for this shortage. **First**, due to the paucity of information on the success or failure of independent releases, NCN-matching is often measured at the scale of an invaded region (9, 10) or at the scale of the whole invaded range (8) i.e. niche shift studies; (8). However, niche shifts can emerge from (i) an initial successful establishment within the NCN followed by spread in novel conditions due to changes in biotic interactions or local adaptation (11), or (ii) a direct establishment outside the NCN (e.g. owing to competition release) and further spread. Therefore, analyses comparing ranges (i.e. instead of introduction sites) to the NCN can yield misleading results concerning the importance of NCN-matching for

establishment. **Second**, factors driving establishment success have mainly been examined at the species level (12), which implies a critical loss of information because the specificities of independent release events are pooled. While summing the number of introduced individuals
65 may be relevant at the species level (13–15), tests of NCN-matching should rather be performed at the level of single release events (16). **Third**, national data are often used to quantify species' NCN, but the use of these restricted datasets may lead to niche truncation issues (17) that could cause NCN-matching underestimation (18). For this reason, NCNs should be assessed globally to ensure taxonomically- and geographically-comprehensive NCN-matching. This has only been
70 performed worldwide for reptiles and amphibians (19) and birds (16). **Fourth**, most NCN-matching metrics used to date captured the differences in latitude between the introduced and native range (20), the inclusion in the same Köppen-Geiger climate class (21), climatic distance to the NCN center (16), or climatic suitability metrics derived from species distribution models (22). However, while these metrics inform about climatic matching inside the NCN, they
75 are not designed to predict how far a site lies outside the NCN (i.e. predictions are floored to zero).

Here, we aim to solve these issues using a new metric - the niche margin index (*NMI*) - and a large release-event dataset for mammals including detailed information on the location and the number of released individuals (23). *NMI* is the first niche metric that accounts for niche
80 *margins*. It is a standardized ecological distance measured between a given site and the closest species' NCN margin (see methods). *NMI* is calculated for all introduction sites and is standardized by the maximum distance to NCN margins in the study area to allow comparison between species presenting different niche sizes (see methods). It thus ranges from $-\infty$ to +1 with negative values representing sites outside the niche (niche outerness), zeroes representing sites at
85 niche margins, and positive values being sites inside the niche (niche innerness) (Fig. 1). We used *NMI* to estimate the climatic-matching of 989 introduction sites to the NCN of 177 alien mammal species. We assessed to what degree *NMI* can explain establishment success, alone and in complement to life-history attributes and historical factors commonly considered in this context (9, 14, 15). For this purpose, we used a Bayesian hierarchical framework from which we
90 extracted posterior distributions of model parameters to assess the strength (median of the posterior distribution) and uncertainty (measured as the 95% Highest Posterior Density interval [HPD₉₅]) of the effect of life-history attributes, historical factors and *NMI* on establishment success. To account for non-independence in the data, we included random effects for the taxonomy and the biogeographic region of introduction (see Methods).



95 **Fig. 1 - Illustration of the Niche margin index (*NMI*).** (A) native distribution, accessible areas (sensu Barve et al. 2011) and alien introductions in geographical space. (B) Schematic representation of *NMI* with distances of introduction sites to native niche margins in the climatic space. (C) Illustration of *NMI* for the ungulate *Alces alces*.

Results and discussion

Establishment was more successful when the colonized sites were inside the NCN, i.e. with
 100 higher *NMI* values (Wilcoxon rank sum test: $U=60603$, $p<1 \times 10^{-6}$, Fig. 2; Bayesian approach:
 posterior $P[NMI>0] = 98.1\%$, effect size = 0.22, $HPD_{95} = [0.01;0.43]$, Fig. 3; see also
 phylogenetic regressions: SOM S3, Fig. S4). Overall, 87.8% (869 out of 989) of introduction
 sites had *NMI* values higher than zero, indicating that most individuals were introduced within
 their NCN. This was true for both successful (715 out of 796) and failed (154 out of 193)
 105 establishments. When tested individually, most species showed a higher *NMI* for sites where
 establishment was successful, but most tests were not significant due to a lack of statistical
 power (Fig. S2).

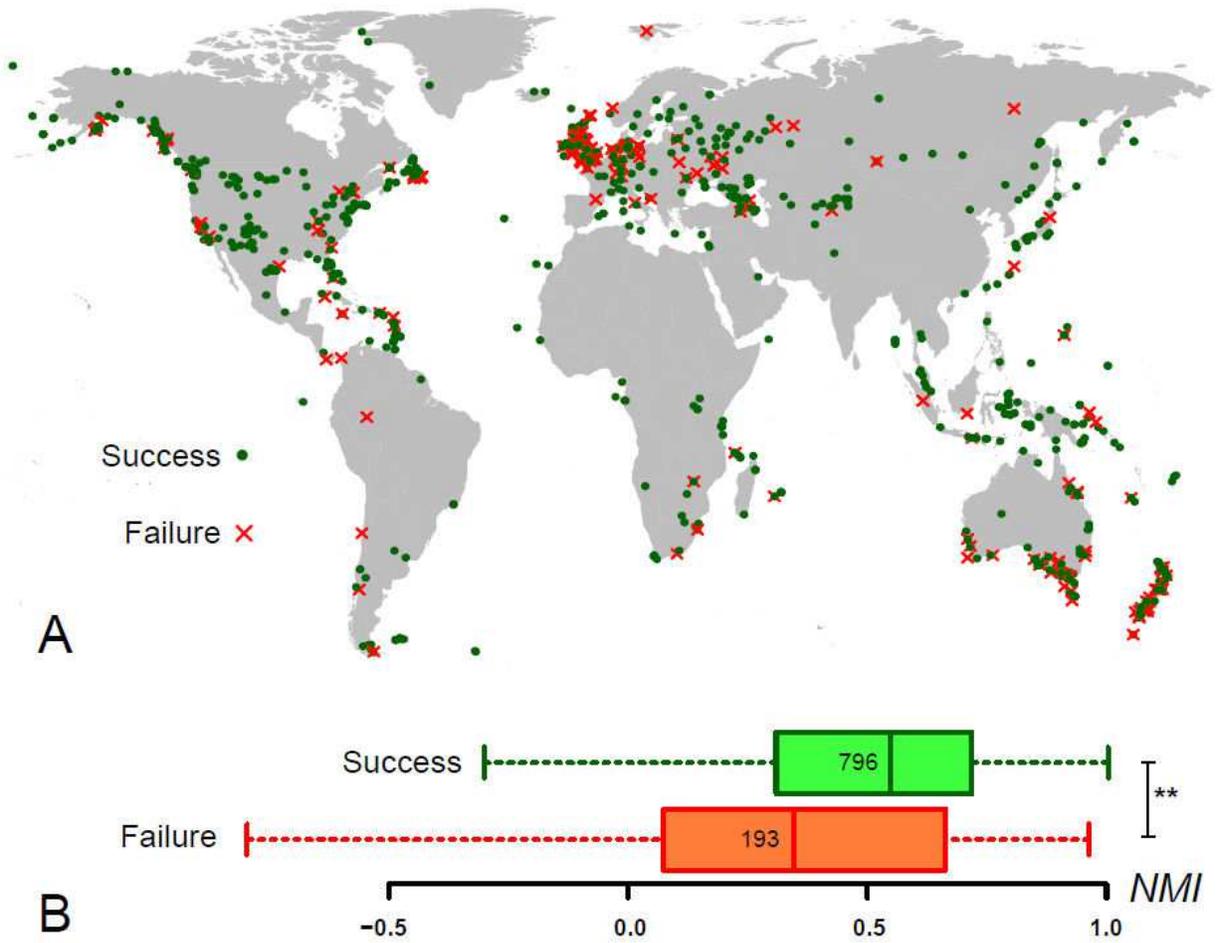


Fig. 2 -NMI and establishment outcome. (A) spatial distribution of successful and failed introductions. (B) *NMI* is significantly higher in successful establishments.

110 Investigations of alien species establishment success have focused primarily on life-history
 attributes (e.g. brain size (24), reproductive lifespans (14), phenotypic plasticity (15)), historical
 factors (e.g. founding population size (25), time since introduction (15)), or characteristics of the
 recipient community (e.g. number of alien species already introduced (13)). Results for many of
 these factors are either inconclusive or highly dependent on the taxonomic group and the study
 115 area (13). Only propagule pressure appears to be a consistent predictor of establishment success
 (26). Here, Bayesian inferences showed that *NMI* had a higher posterior probability for a positive
 effect and a larger effect on establishment success than most of the historical factors and
 life-history attributes classically considered in this context (Fig. 3). Only propagule pressure
 showed stronger evidence for a larger effect size than *NMI* (Fig. 3; $P[\text{effect}>0] = 99.8\%$; effect
 size = 0.60; $\text{HPD}_{95} = [0.15; 1.01]$). The number of litters per year and the coefficient of variation
 120 of neonate body mass also presented positive effects on establishment success ($P[\text{effect}>0] =$
 88% and 92% ; effect size = 0.30 and 0.32, respectively), but uncertainty was higher ($\text{HPD}_{95} =$
 $[-0.23; 0.82]$ and $[-0.12; 0.78]$, respectively), precluding us to draw any firm conclusion (Fig. 3).

These traits may however have a direct impact on population growth by reducing extinction
 125 probability for small populations (25). Beyond confirming the importance of reproductive
 investment and propagule pressure, we show that *NCN*-matching ranks among the most
 important variables to explain establishment success. We reached the same conclusion when
 using a traditional model-based climate suitability index (i.e. predictions obtained from species
 distribution models; see SOM S2; Fig. S6; see also (16)) but at a higher computational cost. Our
 130 findings thus support a systematic use of *NMI*-based climate matching (or equivalent niche
 metrics able to inform how far a site lies outside the *NCN*) in studies assessing establishment
 success.

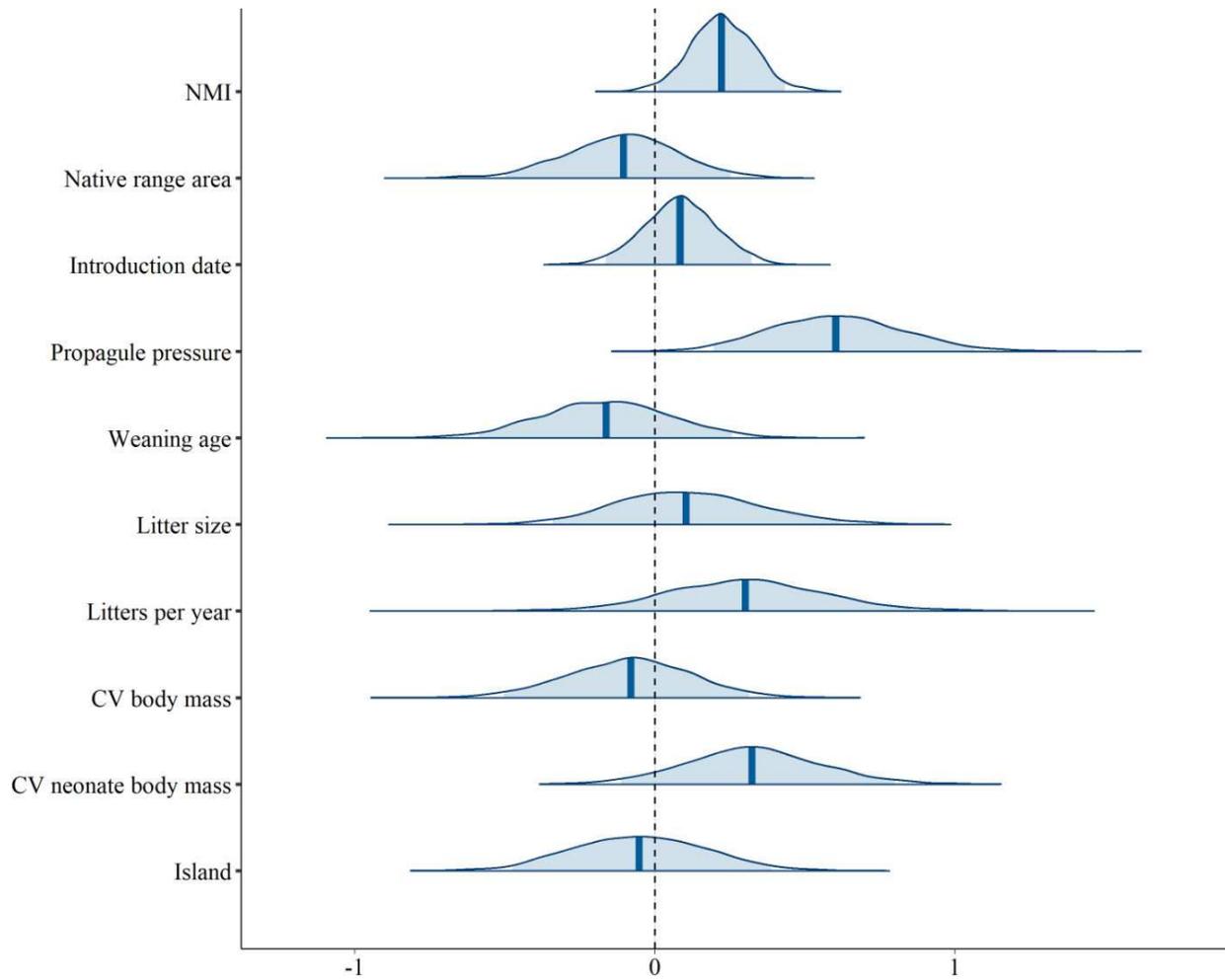


Fig. 3 - Posterior coefficient estimates of the Bayesian model. Distribution of coefficients for fixed effects are shown. Vertical blue lines represent the median of the posterior distribution of effects (i.e. the strength of effect),
 135 while the blue shaded areas under the curves represent the 95% HPD intervals. The vertical dotted line indicates no effect. The posterior probability for a positive effect of the *NMI* on establishment success ($P[NMI > 0]$) equals 98.1%.

Unlike previous niche measures, *NMI* provides key insights for sites located inside (niche innerness) but also, and importantly, outside (niche outerness) niche margins; a characteristic never assessed before. Niche theory predicts that a population can only establish if introduced

140 within the NCN, i.e. within positive *NMI* values. Evidence of niche outerness can however reveal areas where particular evolutionary or ecological processes occur within local populations. *NMI* could also be used to forecast invasion risk owing to e.g. future changes in climatic conditions. For instance, if a given site presents a negative *NMI* in current climatic conditions but a positive (or less negative) value in the future, this would indicate that establishment success at this site is
145 more likely in the future. *NMI* could thus be used as a powerful indicator of where climate change could boost invasions (28). Our results show that most releases of mammals occurred inside the NCN, even for failed establishments. The lack of failed establishment outside the NCN is likely because most reported introductions of mammals were deliberate (874 out of 989 introductions; 88.4%) and people releasing animals probably had an intuitive understanding that
150 climate plays a role in establishment success, and thus likely avoided introducing species in climatically unsuitable areas. If all introductions had been accidental, a larger proportion of sites may have fallen outside the NCN and the signal we detect would have been even stronger. For some species, a few introductions were nevertheless successful outside the NCN. This could be due to several methodological or biological factors. We may for instance have missed climatic
155 (e.g. extreme climatic conditions) or ecological (e.g. habitat use) predictors that may influence the size and the shape of the NCN for some species. It is also possible that biotic interactions, limited available conditions and dispersal limitations in the native range imply that the NCN only provides a partial overview of the climatic conditions that species can tolerate (29). Therefore, some populations might have successfully established outside the NCN due to a release of
160 competition or preadaptation to conditions not present in the native range (27).

Introduction followed by initial establishment is a critical step in the invasion process: once alien species are established, control or eradication becomes difficult and costly (19, 30). Prevention is thus the most cost-effective measure against alien species (30). Confirming an existing, but rarely tested hypothesis (29), we showed that most alien mammals worldwide are more
165 successful at establishing when the climate matches the conditions of their native niche. We further showed that NCN-matching stands among the main predictors for mammal establishment success, which depends on the particular combination of species attributes and release characteristics (31). These results explain why general features of invasions have been difficult to characterize (32). We show that it is nonetheless possible to predict establishment success
170 using NCN-matching, together with propagule pressure and life-history attributes related to reproductive investment. NCN-matching should therefore be systematically included in pre-border invasion risk assessments of environmentally- and economically-damaging biological invaders (33).

Materials and Methods

175 **Introductions data.** From the sections “History of Introductions” for introduced mammals presented in (23), we extracted the 1) geographic coordinates, 2) number and date of release of

introduced individuals and 3) the outcome of each introduction event. John Long compiled this information over a period of 31 years (between 1969 and 2000) from an impressive list of references including peer-reviewed publications, books, governmental and non-governmental reports and conference proceedings all around the world and in many languages. To our knowledge this is still the most complete global dataset on mammal introduction outcomes available. Only populations that were explicitly described as established or expanding were considered as successfully established. Reintroductions in historical parts of the native range of species were not considered. Only species that had no major documented contractions of their range extent during historical times were considered for analysis (but range fragmentations were allowed). This assessment was based on the description of the species in the IUCN Red List database (iucnredlist.org; accessed in November 2013), in particular on information from the “range description” section. We recorded all introduction events for species with fewer than 20 known introductions and the 20 first for species with more than 20 introductions. We chose this threshold of 20 introductions per species to keep the digitalisation work reasonable while keeping all species and a reasonable amount of variability in introductions within each. It resulted in a database of 989 introduction events for 177 mammal species. The number of introduction events varied from one to 36 depending on the species (mean=5.58; SD=7.16). For every introduction we gathered information about historical factors at the release-event level, and life-history attributes at the species level commonly considered in this context (9, 14, 15). Historical factors included introduction date (digitized from (23)), propagule pressure (digitized from (23)), introduction on mainland vs. island (extracted from GADM data shapefile; gadm.org), native range area (extracted from IUCN Red List database shapefile; iucnredlist.org) and the biogeographic region of introduction (extracted from the shapefile of terrestrial ecoregions; maps.tnc.org/gis_data.html). Life-history traits included litter weaning age, litter size, number of litters per year, coefficient of variation of adult body mass and coefficient of variation of neonate body mass (15).

Native climatic niches (NCN). The native ranges of mammal species for which we had introduction events were extracted from the IUCN Red List database (iucnredlist.org) in November 2013. The downloaded shapefiles were converted into a raster at the same resolution as the climatic data (30” which corresponds to about 1 km² at the equator). Using the information contained in the attribute table of the shapefiles, we considered areas labeled as “extant”, “probably extant”, “reintroduced”, “probably extinct” and “extinct” as part of the native range. We used expert-based IUCN range maps to quantify native niches instead of occurrences from GBIF (Global Biodiversity Information Facility; www.gbif.org) because they include areas where the species has disappeared but might be important to quantify the whole native climatic niche (34). The use of GBIF data to quantify niches is further challenged by the fact that these data are spatially biased and prone to identification errors.

To quantify the native climatic niche (NCN) of the species, we used eight bioclimatic variables available worldwide at a resolution of 30” : daily temperature range (tdr), temperature seasonality

(ts), temperature of the coldest quarter (tcoldq), temperature of the warmest quarter (twarmq), precipitation of the driest quarter (pdryq), precipitation of the coldest quarter (pcoldq) and precipitation of the warmest quarter (pwarmq) from worldclim variables (bio2, 4, 10-11 and 16-18 from (35)) and annual aridity (ai, from (36)). These variables are commonly used to
220 quantify the niche of invasive species at global scales (e.g. (37)). We calibrated a principal component analysis (PCA) using the values of all pixels worldwide for the climatic variables (i.e. as the “PCAenv“ in (38)). This PCA provides a reduced climatic space that maximises the climatic variation along principal component axes (Fig. 1B in the main text). The two first axes of the PCA explained 78.33% of the variation and were subsequently used to define the climatic
225 space for the niche quantifications of all species. Note that more axes could be retained to increase the percentage of variation explained in the PCA, but given the high explanatory power of the first two axes, we decided to keep only those two for the ease of representation and interpretation. For each species, we calculated the PCA scores of the pixels belonging to the native niche according to the IUCN. We then transformed these scores into a 100-by-100 grid of
230 the density of occurrence along the PCA axes, thus creating a representation of the native niche in the climatic space (function *ecospat.grid.clim*; R package *ecospat* (39)). We then used the function *rasterToPolygons* (R package *raster*) to transform the raster file into a polygon with boundaries representing the NCN margin (Fig. 1B in the main text).

Niche margin index (*NMI*) as a measure of NCN-matching. We developed a new metric that
235 we called niche margin index (*NMI*; Fig. 1) to measure how far the climatic conditions present at the introduction sites are inside or outside the NCN. The calculation of *NMI* implied 3 steps. 1) We assigned a positive sign to *NMI* if the introduction sites were located inside the NCN, and a negative sign if outside the NCN. 2) We calculated the minimum orthogonal distance of introduction sites to the NCN margin using the *gDistance* function of the R package *rgeos*. Note
240 that this distance is measured here on a plane, but *gDistance* can measure distances in more than two dimensions if more PCA axes are included in the analysis. For single species studies, this distance could be used directly. However, in multi-species studies, *NMI* should be standardized to allow comparison between species presenting different niche sizes. 3) We thus scaled the distance by the maximal orthogonal distance to the margin from anywhere inside the NCN (i.e.
245 the distance to the margin from the “centroid”, defined here as the most distant point from the margin inside the NCN). To achieve this, we generated 10’000 points regularly spaced inside of the NCN using the function *spsample* (R package *sp*) and for each of these points, we calculated the minimum orthogonal distance to the margin. Among all these minimum distances, we selected the longest one and used it as a denominator to scale the distance calculated at step 2).
250 This standardization by the “maximal minimum orthogonal distances” ensures that populations located inside the NCN cannot take a value higher than 1 and that values are comparable across species (i.e. a value of 1 indicates the location the further away from NCN margins, regardless of the size of the NCN). Note however that outside of the NCN, values can be smaller than -1 (when the distance for a site is larger than the distance used for standardization). *NMI* is thus a
255 standardized ecological distance ranging from $-\infty$ to +1 that measures the distance of an

introduced population at a given site (or of any site) to the NCN margin of a species in a climatic space, here defined by the first two axes of a PCA (Fig. 1B). A *NMI* value of +1 indicates that the population was introduced at a site with climatic conditions corresponding to the center of the NCN, a *NMI* value of 0 characterizes locations with climatic conditions at NCN margins, while a highly negative value reflects an introduction at a site where climatic conditions are far outside the NCN.

Statistical analyses. The relationship between establishment success and *NMI* was first assessed individually using a Wilcoxon rank sum test (also known as Mann-Whitney test) and then in conjunction with other explanatory variables commonly used in studies of introduction success (see (14, 15) and references provided in the Introduction section of the main text) using a hierarchical Bayesian mixed-effect model.

a. Model structure

We investigated the effects of *NMI*, species attributes (native range area, weaning age, litter size, litters per year, the coefficient of variation of body mass and the coefficient of variation of neonate body mass) and historical factors (introduction date, propagule pressure and a binary variable indicating whether introductions took place on an island or on the mainland) altogether using Bayesian inference. Specifically, introduction success at site i for species s (denoted $Y_{i(s)}$ to reflect the fact that sites are nested within species) was assumed to follow a Bernoulli distribution with success probability $\psi_{i(s)}$:

$$Y_{i(s)} \sim \text{Bern}(\psi_{i(s)})$$

On the logit scale, $\psi_{i(s)}$ was modelled as :

$$\text{logit}(\psi_{i(s)}) = \alpha + \alpha_{s(fam)} + \alpha_{fam} + \alpha_{region} + \beta \times NMI_{i(s)} + \sum_c^9 \beta_c \times \text{Covariate}_{c,i(s)}$$

where α is the main intercept (i.e. average success probability on the mainland) while $\alpha_{s(fam)}$ are species-wise intercepts nested within family-wise intercepts (denoted α_{fam}) and α_{region} are intercepts associated to biogeographic regions. These three random effects were assumed to be normally distributed with means of zero and standard deviations σ_s , σ_{fam} and σ_{region} , respectively. The parameter β is a slope coefficients representing the effect of the niche margin index ($NMI_{i(s)}$) while parameters β_c are slope coefficients representing the effect of each of the nine above-mentioned covariates ($\text{Covariate}_{c,i(s)}$) on establishment success. $\text{Covariate}_{c,i(s)}$ is a two-dimensional array containing the value of species attributes and historical factors c measured for introduction event i and species s . Note however that some covariates (mostly species life-history attributes) do not vary across sites and are thus assumed to be fixed at the species level. Propagule pressure was log-transformed before analysis to reduce the skewness of its distribution (26). All continuous covariates were standardized to z-scores (mean of zero and

standard deviation of one) before analysis. The correlation between covariates varied from -0.61 to 0.44.

To check the robustness of our results we ran an additional model where we replaced *NMI* by a measure of climatic suitability (CS) obtained from species distribution models (see SOM S2). Very similar results were obtained with this model (SOM Fig. S6).

b. Parameter estimation

Posterior samples of model parameters were obtained by MCMC sampling using JAGS (40) run through the R environment (41) using the package *R2jags* (42). The model was run with two chains with a burn-in of 5,000 and an additional 20,000 iterations with a thinning interval of 20 iterations. For each chain, initial values were selected in different regions of the parameter space.

For fixed intercepts and slope coefficients, we used normal prior distributions with means zero and precision of 0.1 (equivalent to a standard deviation of about 3.1). For standard deviations associated to random intercepts (σ_s , σ_{jam} and σ_{region}), we used half-Cauchy distributions (43). Because most covariates had missing values for some species or sites, we generated new data using Bayesian imputation. Doing so allowed us to conserve and use the information for the other covariates, while producing estimates for the missing values. We followed a MCAR (Missing Completely At Random) procedure, thus assuming the location of missing values in the covariate matrix is completely random with respect to other values (44). In practice, covariates were assumed to follow a normal distribution with mean v_c and standard deviation σ_c (with c varying from one to nine). The priors used for v_c were normal distributions centered on zero with standard deviations of 10, while half-Cauchy distributions were used for σ_c .

All parameters were stored and convergence was assessed using the Gelman and Rubin convergence diagnostic with a threshold fixed to 1.1 (45). For each model, we used posterior predictive checks (46) to assess their goodness of fit. This was done by calculating the sum of squared standardized Pearson residuals for both the observed data and a replicated dataset derived from model estimates. From this χ^2 discrepancy metric, we computed the posterior predictive P-value, which quantifies the proportion of samples in which the distance of observed data to the model is greater than the distance of replicated data to the model. Values close to 0.5 suggest a good model fit, whereas values close to 0 or 1 indicate a lack of fit.

For each parameter, effect sizes were estimated as the median of the corresponding posterior distribution while uncertainties were quantified using the 95% Highest Posterior Density (HPD) interval (function *boa.hpdi*; R package *boa*). For all parameters, we evaluated the posterior probability for the observed effect size (median of the posterior distribution) by calculating the proportion of samples from the posterior distribution displaying the same sign as the observed effect size. For instance, for a positive effect size we calculated the posterior probability for a positive effect (P[$effect > 0$]) by dividing the number of MCMC samples with a positive sign by the total number of MCMC samples. Accordingly, a value of e.g. 0.8 would indicate that the posterior probability for a positive effect is 80% .

The model presented no evidence for convergence issues (potential scale reduction factor below 1.1 for all parameters) and posterior predictive checks revealed no obvious lack of fit (Bayesian p-value=0.22). See SOM Fig. S5 for detailed results.

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Supporting information

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Supporting Text

S1 – Author contributions

OB: co-designed the study, gathered and digitized the introduction data, conceived the innerness index with BP and AG, analyzed the innerness, ran the mixed models and wrote the initial draft of the paper with BP. BP: co-designed the study, gathered the environmental and distributional data, conceived the innerness index with OB and AG, measured innerness and wrote the initial draft of the paper with OB. MC: performed the Bayesian analyses and contributed to write and revise the paper. MG: provided species' trait data and contributed to write and revise the paper. MJM: provided species' trait data and contributed to write and revise the paper. JR: performed the pglms analyses and contributed to write and revise the paper. SMG: contributed to write and revise the paper. SB: co-designed the study, supervised the analyses and contributed to write and revise the paper. AG: co-designed the study, conceived the innerness index with BP and OB, supervised the analyses and contributed to write and revise the paper.

S2 – Influence of climatic suitability (CS) on establishment success

To check the robustness of our results, we repeated our analyses by replacing the niche margin index (NMI) by a traditionally used climatic suitability measure (CS) obtained from species distribution models (SDMs; (17)). SDMs were calibrated for all species using an ensemble modelling approach (18) implemented in the *biomod2* R package (19). The ensemble included three different techniques: generalized linear models (GLM; (20)), gradient boosting machines (GBM; (21)) and maximum entropy (MAXENT; (22)), which were implemented using the default settings of *biomod2*. The same set of climatic variables used for the PCA analyses were used to fit SDMs (23): annual aridity (ai), precipitation of the driest quarter (pdryq), precipitation of the warmest quarter (pwarmq), precipitation of the wettest quarter (pwetq), temperature of the coldest quarter (tcoldq), temperature of the warmest quarter (twarmq), daily range temperature (tdr), and temperature seasonality (ts). The extent of the geographic background was defined as the whole world to allow global extrapolation when projecting the models into new geographic areas. All pixels falling inside the native niche of a species were considered as presences (same dataset as for the native niche in the PCA). We randomly sampled 10,000 pseudo-absences within the geographic background, and weighted presences and absences in the models to ensure a prevalence of 0.5 (24). For each modeling algorithm, 10 iterations of the model were performed. The predictive performance was evaluated using a repeated split-sample approach, with 70% occurrence records used for training the model and 30% for evaluation. Models were evaluated using the true skill statistic (TSS; (25)) across all possible thresholds between 0 and 1 (maxTSS; see (17)). The contribution of variables was evaluated through a permutation procedure: model predictions were recalculated with randomly reshuffled variables, and

Pearson's correlation coefficient was calculated between the initial and reshuffled predictions; 1 minus the correlation provides the contribution of the variable, with 0 indicating that the variable has no influence on the model (function *variables_importance* in *biomod2*). The reshuffling procedure was performed 5 times and correlations were averaged. The overall accuracy of models was excellent, with a mean TSS among species of 0.986 ± 0.011 (SOM Table S1). The variable with the highest average contribution was precipitation in the warmest quarter (0.45 ± 0.163), and the one with the lowest average contribution was aridity (0.105 ± 0.087) (SOM Table S1).

We obtained similar results to NMI with CS (Wilcoxon test: $W = 65253$, $p < 1 \times 10^{-6}$, Bayesian model: Bayesian p-value=0.23; posterior $P[\text{effect of CS} > 0] = 100\%$).

S3 – Influence of NMI on establishment success using phylogenetic regressions

Because it was not possible to implement the complete phylogenetic structure in the hierarchical Bayesian mixed effect model to account for the potential correlation between variables among and within species (because we used Bayesian imputation to deal with missing trait values), we also used phylogenetic logistic regression to test the association between establishment success and NMI.

We used the previously published phylogenetic tree of 5020 species of mammals (26) modified by (27, 28). All species in our dataset were present in the tree except for five species for which we chose the closest representative within the genus (*Equus grevyi* instead of *E. quagga*, *Callosciurus finlaysonii* instead of *C. erythraeus*, *Lama glama* instead of *L. guanicoe*, *Pseudocheirus peregrinus* instead of *P. occidentalis* and *Sciurus griseus* instead of *S. aberti*). We then grafted on this phylogenetic tree of 177 species, 114 individuals inside their respective species in order to provide a tip for each introduction (mean= 7.1 individuals per species, min=1, max= 35). Because the relationships between individuals inside species were not known *a priori*, we generated two distributions of 100 phylogenies. Each tip representing one individual was grafted on the terminal branch of the species given an age drawn from a uniform distribution (between 500 and 10000 years for the first distribution of 100 trees, and between 500 and 50000 years for the second distribution, consistently with ages found in the literature for mammals (29–32)). This grafting procedure was realized using the *multi2di* and the *bind.tip* functions in the R package *ape*.

We fitted a phylogenetic logistic regression described in (33) using the R package *phyloglm* between the introduction success and either NMI or CS. The model was fitted for each tree of the two distributions of 100 phylogenies. Convergence was reached using maximized penalized likelihood of the logistic regression ("logistic_MPLE" using a Firth's correction) for both the

association between success and NMI or CS. The mean p-value for the 100 bootstraps was calculated and we plotted the distribution of p-value for the two distributions of 100 trees.

The detailed results of these analyses can be found in SOM Fig. S2

Table S1 – species-wise SDM results.

The first two columns show the evaluation metrics by TSS. The following columns provide the contribution to the models (see methods) of the following variables: annual aridity (ai), precipitation of the driest quarter (pdryq), precipitation of the warmest quarter (pwarmq), precipitation of the wettest quarter (pwetq), temperature of the coldest quarter (tcoldq), temperature of the warmest quarter (twarmq), daily range temperature (tdr), and temperature seasonality (ts).

	mean	TSS	sd	ai	pdryq	pwarmq	pwetq	tcoldq	tdr	ts	twarmq
	TSS										
<i>Acomys cahirinus</i>	0.987	0.008	0.291	0.007	0.418	0.309	0.146	0.097	0.046	0.224	
<i>Alces alces</i>	0.982	0.007	0.027	0.136	0.252	0.365	0.581	0.196	0.040	0.292	
<i>Alopex lagopus</i>	0.983	0.008	0.030	0.235	0.203	0.522	0.239	0.127	0.035	0.041	
<i>Ammotragus lervia</i>	0.986	0.005	0.135	0.014	0.374	0.311	0.212	0.152	0.010	0.474	
<i>Antilocapra americana</i>	0.990	0.008	0.093	0.441	0.159	0.101	0.213	0.081	0.092	0.092	
<i>Atlantoxerus getulus</i>	0.995	0.004	0.184	0.046	0.506	0.359	0.383	0.281	0.112	0.700	
<i>Axis axis</i>	0.993	0.007	0.094	0.119	0.438	0.542	0.280	0.201	0.027	0.021	
<i>Bandicota indica</i>	0.989	0.006	0.036	0.098	0.520	0.380	0.240	0.336	0.058	0.030	
<i>Bettongia gaimardi</i>	0.999	0.003	0.029	0.057	0.764	0.066	0.454	0.041	0.741	0.418	
<i>Bettongia penicillata</i>	0.995	0.010	0.077	0.138	0.359	0.125	0.401	0.408	0.236	0.830	
<i>Boselaphus tragocamelus</i>	0.994	0.005	0.030	0.053	0.448	0.593	0.271	0.297	0.047	0.022	
<i>Callithrix jacchus</i>	0.994	0.006	0.086	0.026	0.646	0.275	0.182	0.074	0.054	0.090	
<i>Callosciurus erythraeus</i>	0.988	0.008	0.039	0.089	0.435	0.250	0.262	0.165	0.076	0.269	
<i>Canis aureus</i>	0.959	0.009	0.004	0.018	0.510	0.467	0.175	0.027	0.076	0.175	
<i>Capra ibex</i>	0.996	0.007	0.073	0.169	0.468	0.431	0.476	0.204	0.573	0.262	
<i>Capreolus capreolus</i>	0.990	0.006	0.028	0.186	0.356	0.241	0.431	0.085	0.068	0.066	
<i>Castor canadensis</i>	0.970	0.010	0.028	0.222	0.553	0.402	0.374	0.089	0.337	0.064	
<i>Cebus albifrons</i>	0.987	0.007	0.025	0.040	0.843	0.045	0.092	0.089	0.044	0.088	
<i>Cebus apella</i>	0.992	0.006	0.054	0.017	0.365	0.157	0.294	0.385	0.173	0.021	
<i>Cercopithecus mona</i>	0.996	0.004	0.196	0.112	0.757	0.184	0.108	0.061	0.047	0.049	
<i>Cervus elaphus</i>	0.950	0.022	0.092	0.020	0.383	0.211	0.623	0.204	0.087	0.013	
<i>Chlorocebus aethiops</i>	0.990	0.004	0.023	0.198	0.508	0.198	0.588	0.017	0.037	0.135	
<i>Connochaetes taurinus</i>	0.989	0.007	0.141	0.023	0.375	0.278	0.451	0.043	0.058	0.055	
<i>Crocidura suaveolens</i>	0.977	0.008	0.370	0.193	0.345	0.230	0.445	0.164	0.069	0.125	

<i>Dasyprocta leporina</i>	0.994	0.005	0.063	0.136	0.496	0.059	0.215	0.306	0.127	0.014
<i>Dasybus novemcinctus</i>	0.965	0.009	0.027	0.046	0.145	0.137	0.585	0.072	0.098	0.050
<i>Daubentonia madagascariensis</i>	0.995	0.007	0.225	0.058	0.745	0.229	0.216	0.418	0.189	0.544
<i>Dendrolagus matschiei</i>	0.995	0.010	0.081	0.220	0.732	0.184	0.178	0.134	0.232	0.800
<i>Didelphis marsupialis</i>	0.983	0.007	0.026	0.009	0.627	0.177	0.358	0.051	0.073	0.010
<i>Dipodomys ordii</i>	0.992	0.006	0.078	0.366	0.349	0.257	0.389	0.032	0.169	0.062
<i>Equus quagga</i>	0.979	0.007	0.195	0.012	0.450	0.126	0.123	0.046	0.022	0.052
<i>Erinaceus europaeus</i>	0.990	0.004	0.213	0.214	0.354	0.175	0.212	0.142	0.086	0.019
<i>Eulemur coronatus</i>	0.999	0.005	0.626	0.164	0.551	0.015	0.075	0.324	0.101	0.763
<i>Eulemur fulvus</i>	0.998	0.003	0.246	0.087	0.767	0.247	0.230	0.716	0.084	0.467
<i>Eulemur mongoz</i>	1.000	0.003	0.296	0.007	0.234	0.125	0.241	0.946	0.459	0.080
<i>Euphractus sexcinctus</i>	0.977	0.009	0.039	0.050	0.368	0.189	0.453	0.061	0.037	0.022
<i>Funambulus pennantii</i>	0.989	0.006	0.071	0.023	0.442	0.667	0.269	0.173	0.076	0.024
<i>Genetta genetta</i>	0.971	0.007	0.103	0.013	0.317	0.157	0.570	0.025	0.051	0.069
<i>Giraffa camelopardalis</i>	0.976	0.008	0.134	0.019	0.295	0.150	0.541	0.050	0.067	0.052
<i>Glis glis</i>	0.991	0.005	0.104	0.273	0.367	0.329	0.519	0.130	0.191	0.030
<i>Hemitragus jemlahicus</i>	0.995	0.006	0.233	0.209	0.694	0.597	0.366	0.400	0.108	0.119
<i>Herpestes edwardsii</i>	0.985	0.008	0.119	0.086	0.445	0.579	0.245	0.231	0.049	0.007
<i>Herpestes ichneumon</i>	0.963	0.010	0.014	0.002	0.535	0.216	0.498	0.029	0.088	0.047
<i>Herpestes javanicus</i>	0.966	0.014	0.081	0.050	0.521	0.441	0.307	0.269	0.143	0.047
<i>Hippopotamus amphibius</i>	0.958	0.009	0.022	0.005	0.453	0.125	0.413	0.012	0.046	0.030
<i>Hippotragus equinus</i>	0.988	0.008	0.195	0.045	0.359	0.140	0.295	0.062	0.118	0.021
<i>Hylobates lar</i>	0.984	0.009	0.060	0.154	0.630	0.236	0.149	0.285	0.131	0.257
<i>Hystrix brachyura</i>	0.985	0.006	0.022	0.185	0.465	0.326	0.273	0.145	0.081	0.278
<i>Isodon auratus</i>	0.997	0.007	0.277	0.599	0.487	0.329	0.563	0.379	0.136	0.014
<i>Isodon obesulus</i>	0.995	0.005	0.072	0.075	0.683	0.168	0.500	0.120	0.085	0.163
<i>Kobus kob</i>	0.990	0.008	0.091	0.062	0.313	0.097	0.512	0.080	0.005	0.070
<i>Kobus leche</i>	0.994	0.007	0.135	0.205	0.226	0.341	0.470	0.122	0.515	0.047
<i>Lama guanicoe</i>	0.990	0.008	0.073	0.014	0.538	0.292	0.381	0.061	0.045	0.039
<i>Lasiorhinus latifrons</i>	0.997	0.006	0.028	0.016	0.275	0.142	0.429	0.165	0.531	0.721
<i>Leporillus conditor</i>	0.993	0.012	0.284	0.134	0.207	0.075	0.266	0.600	0.579	0.735
<i>Lepus americanus</i>	0.977	0.005	0.053	0.095	0.466	0.605	0.361	0.124	0.308	0.122
<i>Lepus arcticus</i>	0.990	0.007	0.032	0.385	0.193	0.281	0.533	0.076	0.043	0.139

<i>Lepus californicus</i>	0.978	0.008	0.017	0.374	0.313	0.161	0.420	0.010	0.050	0.029
<i>Lepus europaeus</i>	0.975	0.010	0.208	0.226	0.409	0.359	0.485	0.141	0.109	0.097
<i>Lepus nigricollis</i>	0.991	0.006	0.010	0.069	0.246	0.620	0.246	0.099	0.026	0.032
<i>Lepus timidus</i>	0.976	0.008	0.140	0.049	0.449	0.295	0.325	0.195	0.117	0.262
<i>Loxodonta africana</i>	0.967	0.009	0.018	0.002	0.433	0.125	0.409	0.053	0.040	0.025
<i>Lycaon pictus</i>	0.975	0.009	0.101	0.015	0.216	0.083	0.573	0.069	0.147	0.039
<i>Lynx lynx</i>	0.961	0.009	0.029	0.048	0.216	0.246	0.689	0.025	0.135	0.033
<i>Macaca arctoides</i>	0.990	0.007	0.061	0.121	0.451	0.180	0.156	0.241	0.119	0.181
<i>Macaca cyclopis</i>	1.000	0.003	0.058	0.645	0.496	0.138	0.141	0.022	0.028	0.831
<i>Macaca fascicularis</i>	0.987	0.007	0.027	0.213	0.576	0.198	0.212	0.180	0.031	0.172
<i>Macaca fuscata</i>	0.997	0.006	0.281	0.033	0.470	0.318	0.315	0.041	0.274	0.528
<i>Macaca mulatta</i>	0.986	0.006	0.023	0.009	0.606	0.376	0.303	0.407	0.118	0.030
<i>Macaca nemestrina</i>	0.994	0.007	0.098	0.131	0.662	0.170	0.084	0.067	0.243	0.285
<i>Macaca nigra</i>	1.000	0.000	0.051	0.000	0.000	0.067	0.060	0.002	0.000	0.144
<i>Macropus agilis</i>	0.994	0.005	0.235	0.082	0.571	0.399	0.231	0.272	0.077	0.311
<i>Macropus dorsalis</i>	0.995	0.007	0.304	0.043	0.615	0.273	0.255	0.162	0.299	0.340
<i>Macropus fuliginosus</i>	0.996	0.006	0.070	0.014	0.387	0.197	0.489	0.028	0.178	0.183
<i>Macropus giganteus</i>	0.987	0.007	0.188	0.041	0.602	0.272	0.332	0.044	0.186	0.094
<i>Macropus parma</i>	0.997	0.007	0.065	0.029	0.584	0.297	0.276	0.057	0.650	0.393
<i>Macropus robustus</i>	0.988	0.008	0.206	0.041	0.385	0.115	0.207	0.041	0.075	0.079
<i>Macropus rufogriseus</i>	0.994	0.005	0.176	0.039	0.658	0.197	0.398	0.162	0.449	0.008
<i>Marmota bobak</i>	0.995	0.005	0.166	0.085	0.597	0.336	0.320	0.143	0.186	0.014
<i>Marmota camtschatica</i>	0.983	0.006	0.044	0.039	0.480	0.568	0.273	0.150	0.116	0.175
<i>Marmota monax</i>	0.986	0.005	0.117	0.175	0.295	0.120	0.209	0.064	0.317	0.121
<i>Martes americana</i>	0.979	0.005	0.093	0.084	0.458	0.678	0.278	0.160	0.292	0.132
<i>Martes martes</i>	0.987	0.006	0.078	0.209	0.249	0.154	0.363	0.145	0.090	0.069
<i>Martes melampus</i>	0.998	0.004	0.207	0.024	0.487	0.304	0.334	0.013	0.257	0.518
<i>Martes pennanti</i>	0.980	0.005	0.047	0.185	0.325	0.479	0.316	0.112	0.289	0.107
<i>Meles meles</i>	0.988	0.006	0.024	0.226	0.197	0.072	0.370	0.085	0.022	0.128
<i>Mephitis mephitis</i>	0.978	0.007	0.033	0.371	0.457	0.292	0.376	0.031	0.232	0.027
<i>Meriones unguiculatus</i>	0.988	0.007	0.088	0.088	0.314	0.270	0.480	0.081	0.292	0.213
<i>Moschus moschiferus</i>	0.990	0.006	0.069	0.088	0.483	0.229	0.450	0.070	0.112	0.111
<i>Mungos mungo</i>	0.977	0.007	0.078	0.004	0.458	0.203	0.546	0.036	0.063	0.013

<i>Muntiacus muntjak</i>	0.992	0.007	0.038	0.141	0.558	0.060	0.027	0.224	0.153	0.233
<i>Muntiacus reevesi</i>	0.996	0.007	0.054	0.277	0.295	0.069	0.190	0.117	0.010	0.418
<i>Muscardinus avellanarius</i>	0.992	0.006	0.071	0.301	0.246	0.251	0.391	0.167	0.212	0.011
<i>Mustela erminea</i>	0.986	0.007	0.012	0.007	0.202	0.143	0.285	0.018	0.086	0.042
<i>Mustela nivalis</i>	0.985	0.007	0.057	0.070	0.582	0.399	0.369	0.075	0.024	0.016
<i>Mustela putorius</i>	0.991	0.006	0.040	0.272	0.381	0.311	0.377	0.123	0.134	0.027
<i>Mustela sibirica</i>	0.979	0.006	0.049	0.038	0.322	0.312	0.508	0.062	0.110	0.441
<i>Myocastor coypus</i>	0.983	0.007	0.057	0.032	0.627	0.187	0.318	0.012	0.069	0.033
<i>Myodes glareolus</i>	0.989	0.008	0.062	0.254	0.270	0.305	0.454	0.075	0.142	0.037
<i>Myodes rutilus</i>	0.973	0.008	0.029	0.045	0.258	0.267	0.499	0.012	0.078	0.039
<i>Myrmecobius fasciatus</i>	0.998	0.005	0.060	0.151	0.320	0.242	0.443	0.057	0.697	0.800
<i>Nasua nasua</i>	0.985	0.007	0.144	0.075	0.392	0.166	0.361	0.073	0.040	0.009
<i>Neovison vison</i>	0.970	0.011	0.118	0.137	0.594	0.471	0.320	0.158	0.387	0.086
<i>Nesotragus moschatus</i>	0.989	0.006	0.177	0.047	0.559	0.161	0.328	0.163	0.025	0.121
<i>Nyctereutes procyonoides</i>	0.992	0.007	0.093	0.075	0.286	0.053	0.147	0.219	0.149	0.471
<i>Nycticebus coucang</i>	0.994	0.006	0.059	0.155	0.685	0.197	0.103	0.296	0.368	0.418
<i>Odocoileus hemionus</i>	0.980	0.006	0.150	0.379	0.415	0.353	0.411	0.031	0.107	0.156
<i>Odocoileus virginianus</i>	0.946	0.014	0.042	0.348	0.284	0.189	0.324	0.084	0.329	0.083
<i>Ondatra zibethicus</i>	0.973	0.009	0.014	0.196	0.532	0.410	0.414	0.072	0.350	0.066
<i>Onychogalea unguifera</i>	0.996	0.007	0.207	0.003	0.225	0.267	0.490	0.100	0.244	0.263
<i>Oreamnos americanus</i>	0.992	0.005	0.108	0.130	0.407	0.665	0.322	0.034	0.191	0.060
<i>Ornithorhynchus anatinus</i>	0.992	0.006	0.138	0.031	0.701	0.249	0.331	0.086	0.342	0.053
<i>Oryx gazella</i>	0.995	0.005	0.236	0.036	0.338	0.210	0.257	0.053	0.136	0.030
<i>Ovibos moschatus</i>	0.993	0.006	0.049	0.180	0.111	0.372	0.280	0.034	0.031	0.200
<i>Ovis ammon</i>	0.989	0.006	0.172	0.071	0.176	0.037	0.542	0.074	0.111	0.064
<i>Ovis canadensis</i>	0.984	0.006	0.170	0.341	0.328	0.112	0.351	0.203	0.095	0.197
<i>Paguma larvata</i>	0.979	0.007	0.091	0.143	0.481	0.303	0.299	0.224	0.069	0.355
<i>Pan troglodytes</i>	0.983	0.007	0.202	0.003	0.561	0.081	0.314	0.011	0.011	0.006
<i>Paradoxurus hermaphroditus</i>	0.982	0.006	0.031	0.137	0.597	0.336	0.172	0.382	0.054	0.054
<i>Parantechinus apicalis</i>	1.000	0.000	0.177	0.173	0.393	0.189	0.331	0.083	0.777	0.714
<i>Perameles gunnii</i>	0.997	0.006	0.053	0.045	0.763	0.185	0.474	0.068	0.802	0.455
<i>Peromyscus maniculatus</i>	0.971	0.007	0.136	0.391	0.430	0.318	0.352	0.029	0.177	0.056
<i>Petaurus breviceps</i>	0.977	0.011	0.220	0.064	0.660	0.277	0.259	0.185	0.237	0.181

<i>Petrogale penicillata</i>	0.997	0.005	0.205	0.201	0.643	0.291	0.335	0.138	0.721	0.290
<i>Phascolarctos cinereus</i>	0.990	0.007	0.085	0.030	0.662	0.245	0.306	0.086	0.219	0.056
<i>Potamochoerus porcus</i>	0.985	0.007	0.154	0.003	0.475	0.068	0.347	0.049	0.013	0.006
<i>Potorous tridactylus</i>	0.996	0.006	0.110	0.054	0.761	0.281	0.418	0.149	0.630	0.011
<i>Procapra gutturosa</i>	0.995	0.007	0.030	0.158	0.294	0.141	0.341	0.073	0.388	0.054
<i>Procolobus kirkii</i>	0.997	0.018	0.354	0.281	0.574	0.368	0.516	0.395	0.427	0.107
<i>Procyon lotor</i>	0.951	0.013	0.031	0.387	0.351	0.197	0.243	0.067	0.210	0.020
<i>Pseudalopex griseus</i>	0.990	0.006	0.047	0.010	0.722	0.210	0.459	0.027	0.085	0.064
<i>Pseudocheirus occidentalis</i>	0.999	0.004	0.134	0.035	0.393	0.290	0.391	0.252	0.145	0.681
<i>Pseudois nayaur</i>	0.996	0.007	0.128	0.026	0.349	0.264	0.231	0.031	0.165	0.085
<i>Rangifer tarandus</i>	0.981	0.008	0.044	0.045	0.072	0.319	0.427	0.005	0.042	0.035
<i>Rattus argentiventer</i>	0.989	0.007	0.046	0.228	0.349	0.094	0.210	0.255	0.034	0.162
<i>Rattus nitidus</i>	0.990	0.007	0.061	0.020	0.463	0.328	0.329	0.087	0.102	0.337
<i>Rattus praetor</i>	0.996	0.005	0.038	0.238	0.397	0.091	0.143	0.025	0.672	0.569
<i>Rattus tanezumi</i>	0.985	0.006	0.078	0.093	0.270	0.194	0.313	0.249	0.159	0.385
<i>Rhinolophus ferrumequinum</i>	0.974	0.007	0.067	0.106	0.490	0.278	0.487	0.155	0.024	0.076
<i>Rhizomys sumatrensis</i>	0.985	0.007	0.067	0.137	0.529	0.194	0.167	0.273	0.105	0.239
<i>Rupicapra rupicapra</i>	0.992	0.006	0.062	0.129	0.552	0.411	0.442	0.274	0.236	0.061
<i>Rusa timorensis</i>	0.994	0.011	0.265	0.094	0.773	0.087	0.124	0.319	0.268	0.724
<i>Rusa unicolor</i>	0.985	0.005	0.039	0.121	0.594	0.345	0.221	0.462	0.060	0.082
<i>Saimiri sciureus</i>	0.990	0.008	0.064	0.017	0.572	0.001	0.022	0.099	0.111	0.017
<i>Sciurus aberti</i>	0.993	0.008	0.190	0.509	0.450	0.372	0.340	0.142	0.221	0.105
<i>Sciurus carolinensis</i>	0.995	0.005	0.118	0.121	0.449	0.316	0.264	0.046	0.405	0.130
<i>Sciurus niger</i>	0.993	0.007	0.098	0.184	0.405	0.325	0.235	0.092	0.174	0.104
<i>Sciurus vulgaris</i>	0.970	0.008	0.066	0.080	0.269	0.316	0.534	0.069	0.071	0.093
<i>Sorex cinereus</i>	0.973	0.011	0.101	0.080	0.451	0.447	0.461	0.123	0.306	0.065
<i>Spermophilus beecheyi</i>	0.995	0.006	0.149	0.104	0.374	0.270	0.451	0.064	0.074	0.516
<i>Spermophilus major</i>	0.993	0.008	0.182	0.233	0.295	0.091	0.602	0.197	0.119	0.180
<i>Spermophilus parryii</i>	0.979	0.005	0.044	0.122	0.438	0.744	0.220	0.042	0.039	0.106
<i>Spilocuscus maculatus</i>	0.993	0.008	0.045	0.196	0.551	0.068	0.043	0.104	0.181	0.602
<i>Suncus etruscus</i>	0.959	0.010	0.081	0.254	0.374	0.224	0.635	0.020	0.063	0.035
<i>Suncus murinus</i>	0.980	0.006	0.061	0.171	0.527	0.420	0.207	0.429	0.040	0.053
<i>Sus scrofa</i>	0.951	0.013	0.203	0.245	0.171	0.240	0.457	0.243	0.072	0.030

<i>Sylvilagus floridanus</i>	0.962	0.014	0.033	0.219	0.199	0.313	0.287	0.047	0.163	0.076
<i>Tachyglossus aculeatus</i>	0.982	0.013	0.208	0.033	0.441	0.200	0.394	0.047	0.080	0.064
<i>Talpa europaea</i>	0.992	0.007	0.040	0.319	0.344	0.315	0.338	0.092	0.208	0.025
<i>Tamias sibiricus</i>	0.977	0.006	0.185	0.027	0.390	0.100	0.128	0.182	0.198	0.436
<i>Tamias striatus</i>	0.996	0.006	0.014	0.106	0.390	0.307	0.346	0.077	0.304	0.178
<i>Tamias townsendii</i>	0.996	0.008	0.074	0.032	0.191	0.429	0.346	0.480	0.249	0.377
<i>Tamiasciurus hudsonicus</i>	0.974	0.008	0.066	0.135	0.472	0.466	0.430	0.062	0.317	0.067
<i>Tayassu pecari</i>	0.979	0.007	0.043	0.028	0.349	0.149	0.483	0.055	0.045	0.006
<i>Tenrec ecaudatus</i>	0.995	0.006	0.181	0.006	0.607	0.077	0.122	0.184	0.061	0.548
<i>Thylogale browni</i>	0.994	0.007	0.011	0.027	0.652	0.093	0.081	0.020	0.377	0.616
<i>Trachypithecus auratus</i>	0.993	0.006	0.151	0.172	0.701	0.072	0.177	0.694	0.184	0.285
<i>Tragelaphus strepsiceros</i>	0.977	0.007	0.160	0.013	0.398	0.195	0.517	0.015	0.034	0.024
<i>Trichosurus vulpecula</i>	0.978	0.009	0.168	0.039	0.548	0.200	0.364	0.109	0.107	0.065
<i>Varecia variegata</i>	0.997	0.007	0.045	0.087	0.634	0.121	0.045	0.142	0.035	0.957
<i>Viverra tangalunga</i>	0.991	0.008	0.060	0.146	0.483	0.040	0.027	0.111	0.040	0.174
<i>Viverra zibetha</i>	0.989	0.007	0.088	0.052	0.502	0.311	0.255	0.189	0.091	0.237
<i>Viverricula indica</i>	0.985	0.006	0.075	0.108	0.512	0.389	0.264	0.418	0.068	0.082
<i>Vulpes vulpes</i>	0.984	0.006	0.015	0.100	0.554	0.183	0.434	0.069	0.022	0.010
<i>Wallabia bicolor</i>	0.991	0.006	0.181	0.045	0.725	0.315	0.303	0.110	0.274	0.069
<i>Zaedyus pichiy</i>	0.995	0.005	0.006	0.023	0.738	0.172	0.490	0.003	0.076	0.080
Mean	0.986	0.007	0.105	0.124	0.450	0.257	0.332	0.146	0.172	0.187
Sd	0.011	0.003	0.087	0.118	0.163	0.146	0.141	0.14	0.169	0.216

Figs. S1 to S3

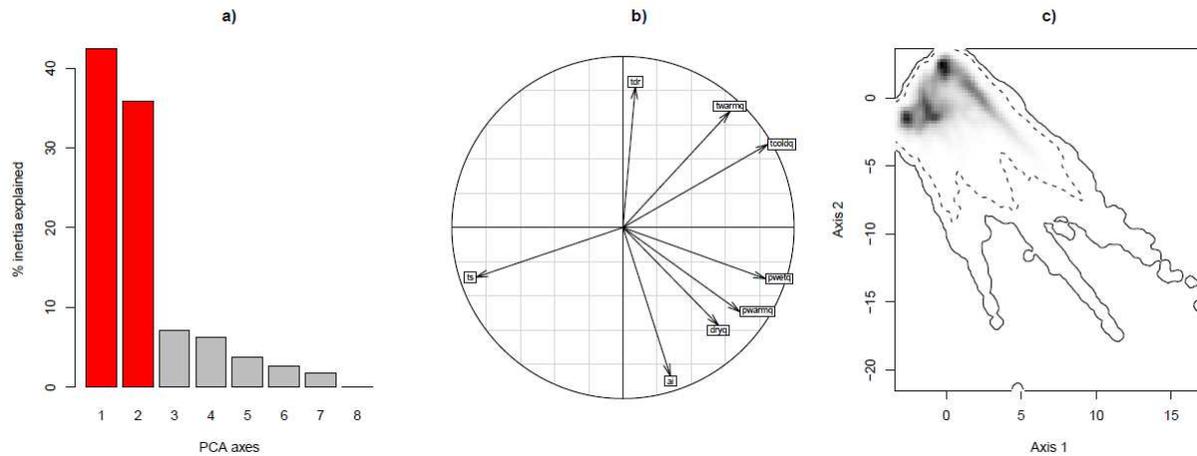


Fig. S1- PCA results.

a) Inertia explained by the PCA axes. The first and second axes explain 42.50 % and 35.83% of the inertia of the PCA, respectively. b) Correlation circle showing the contribution of initial variables to PCA axes (ai = aridity index, tdr = daily temperature range, ts = temperature seasonality, tcoldq = temperature of the coldest quarter, twarmq = temperature of the warmest quarter, pdryq = precipitation of the driest quarter, pcoldq = precipitation of the coldest quarter, pwarmq = precipitation of the warmest quarter) c) climatic space along the two first PCA axes with the density of climate worldwide in gray (black = most common climates).

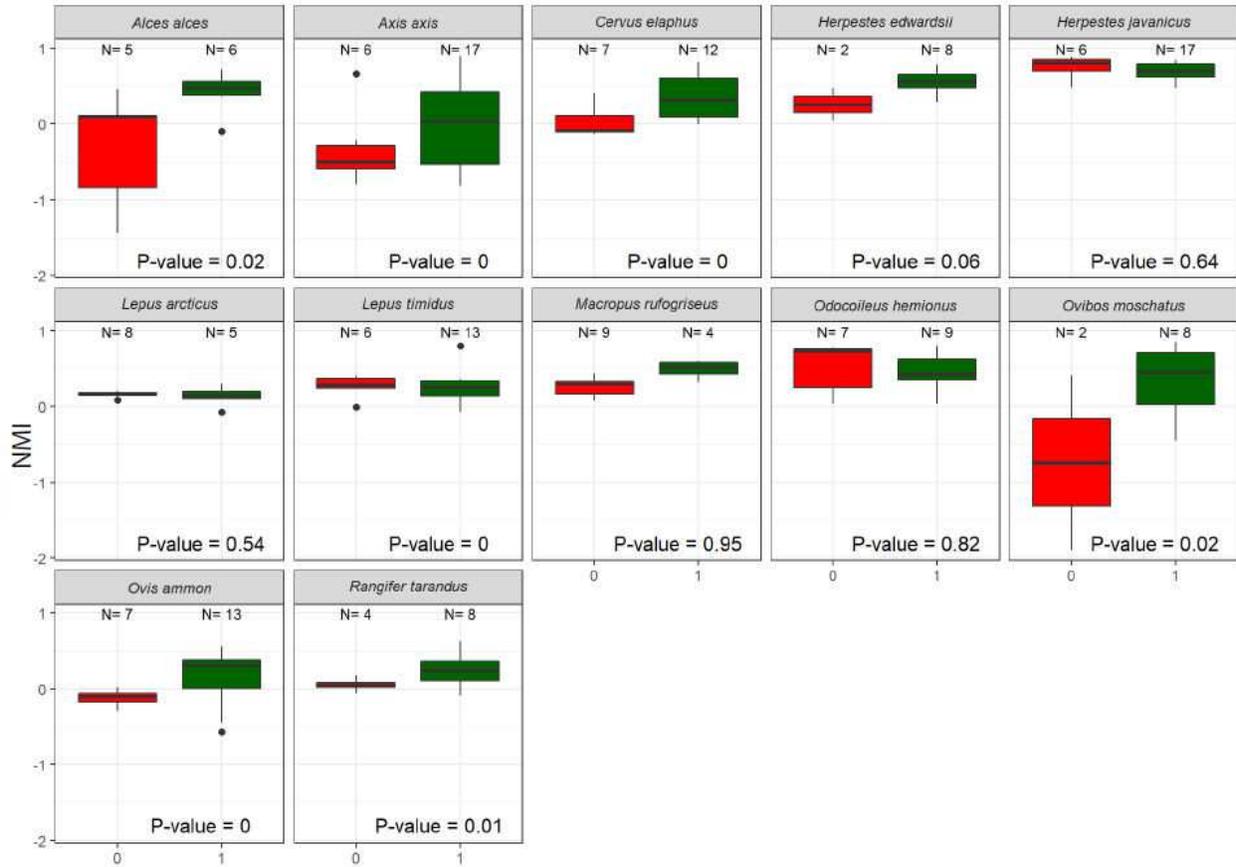


Fig. S2 – Influence of NMI on introduction success for individual species.

Only species with number of introductions >9 and ratio introduction success/introduction failure between 0.2 and 5 are shown. P-values are for Wilcoxon tests.

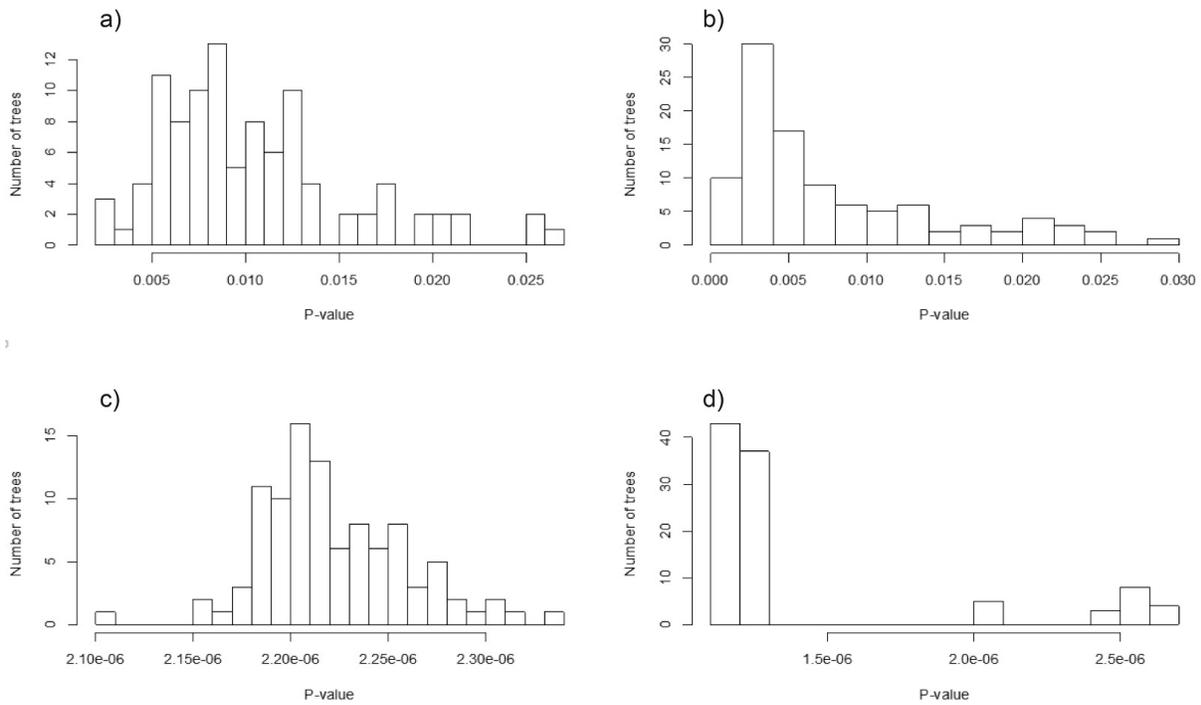


Figure S3 – Phylogenetic logistic regressions.

Distributions of the p-values for the phylogenetic logistic regressions relating establishment success to the niche margin index (NMI; a,b), and establishment success to climatic suitability (CS; c,d). For each relationship, 100 phylogenetic trees were created by grafting individuals on the terminal branch of their species given an age randomly drawn from a uniform distribution between 500 and 10'000 years (a,c) and between 500 and 50'000 yrs (b,d). In all simulations, the model shows a significant relationship (p-value < 0.05).

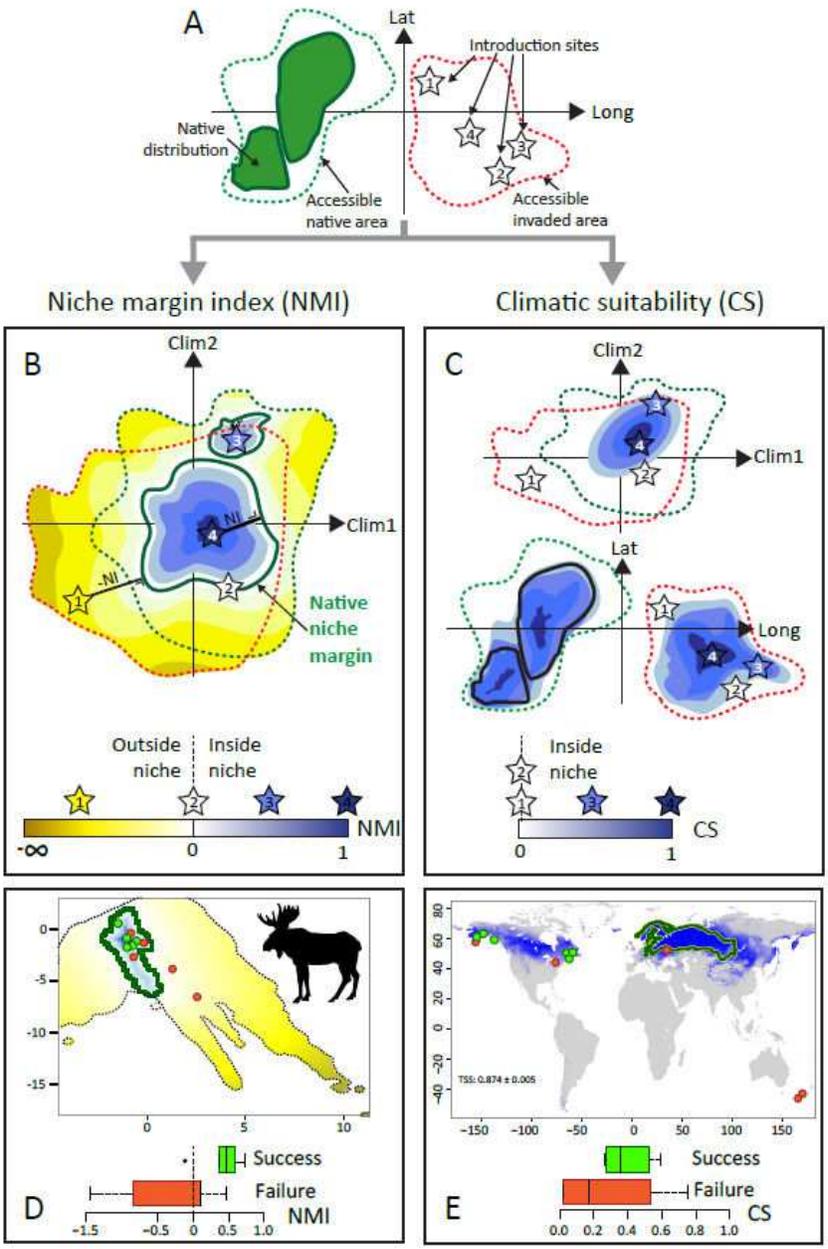


Figure S4 – Schematic representation of NMI and CS as metrics of NCN-matching

(A) native distribution, accessible areas (sensu Barve et al. 2011) and exotic introduction in geographical space. (B) Schematic representation of the niche margin index (NMI) with distances of introduction sites to native niche margins in climatic space. (C) Climatic suitability (CS) of introduction sites in climatic and geographic space. Introductions outside the native niche are floored to 0 for CS. (D) and (E) Illustration of NMI and CS for the Elk (*Alces alces*).

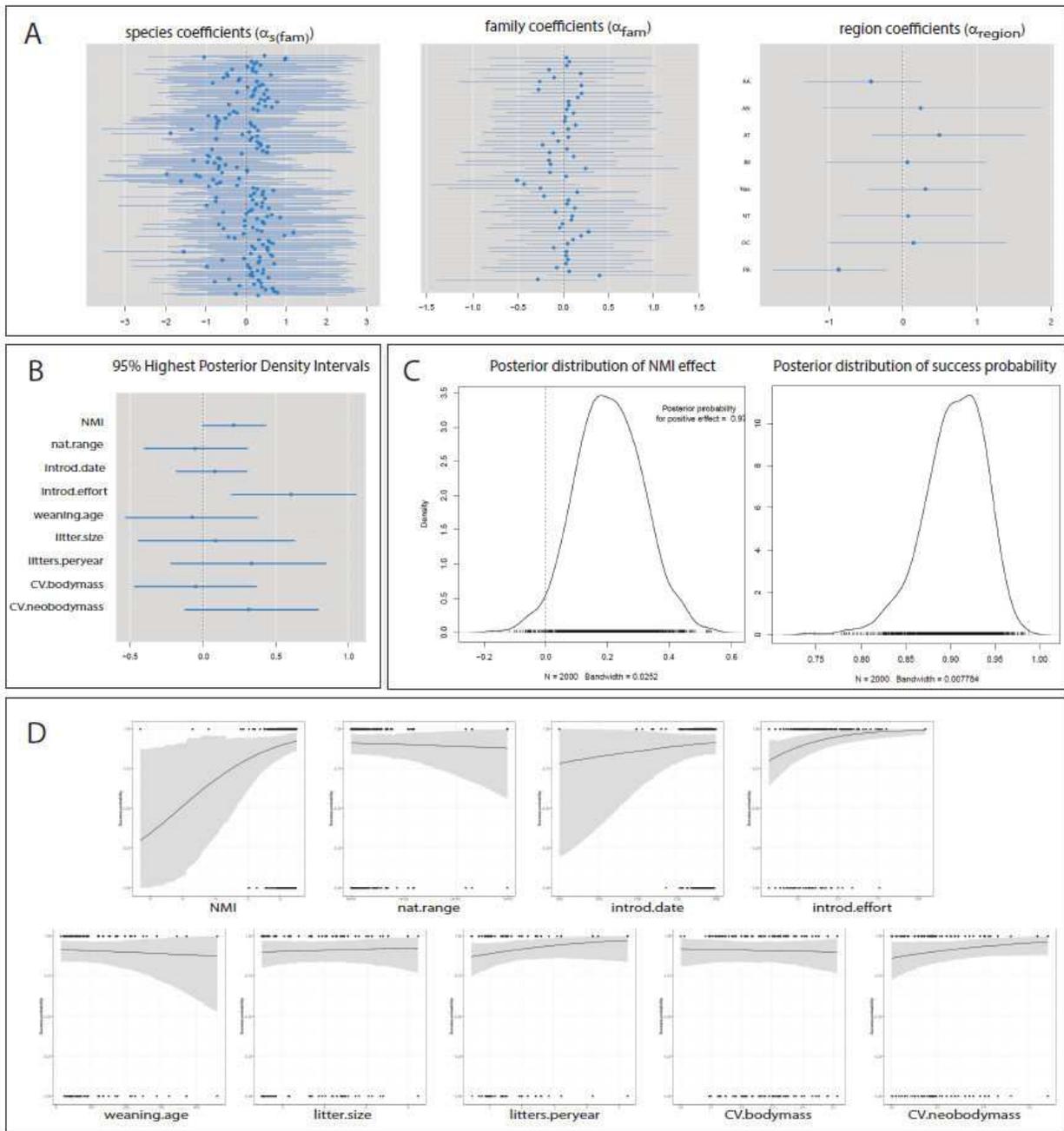


Figure S5 – Detailed results of the Bayesian hierarchical mixed effect model for NMI.

(A) coefficients of the random factors (on a logit scale). (B) 95% highest posterior density intervals of fixed factors (on a logit scale). (C) Posterior distribution of NMI and success probability. (D) Response curve and 95% credible interval of establishment success probability as a function of the fixed factors.

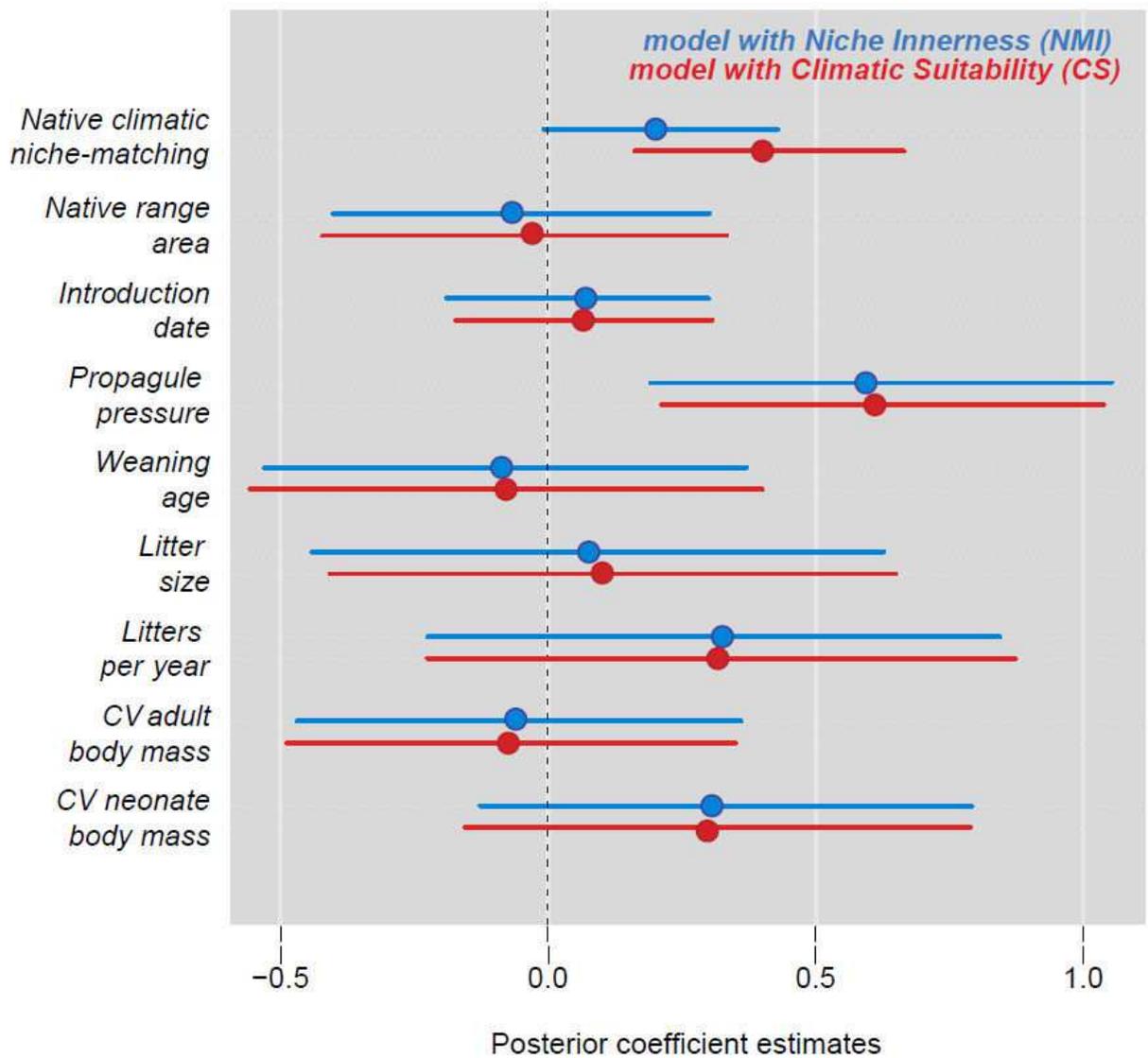


Figure S6 – Posterior coefficients of the Bayesian models.

Horizontal bars represent the 95% highest posterior density intervals for fixed effects. Dots represent the median of the posterior distribution of effects. The vertical dotted line indicates no effect.

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Figures

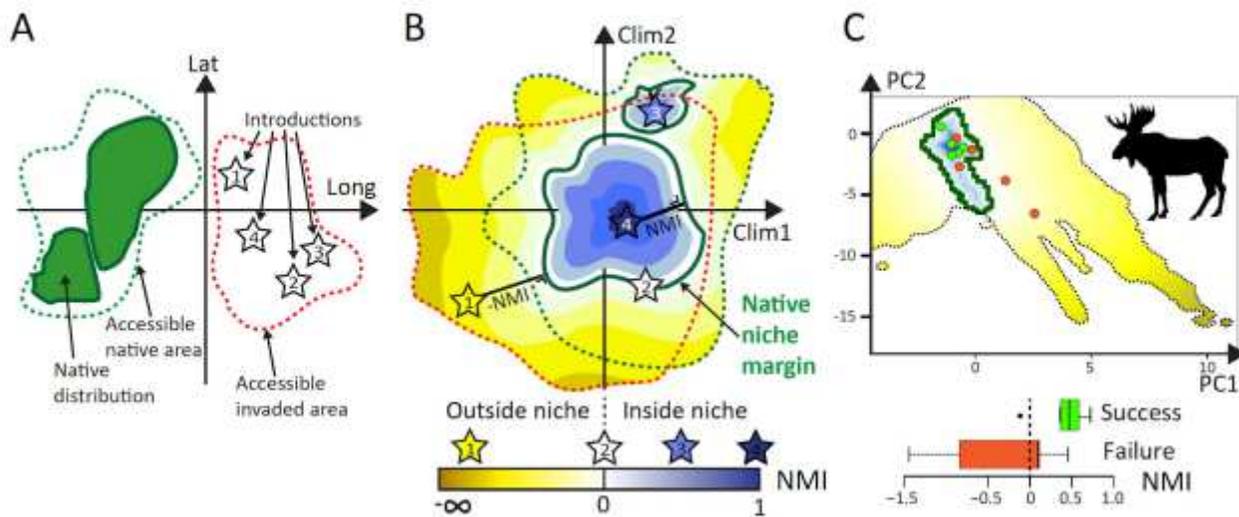


Figure 1

Illustration of the Niche margin index (NMI). (A) native distribution, accessible areas (sensu Barve et al. 2011) and alien introductions in geographical space. (B) Schematic representation of NMI with distances of introduction sites to native niche margins in the climatic space. (C) Illustration of NMI for the ungulate *Alces alces*

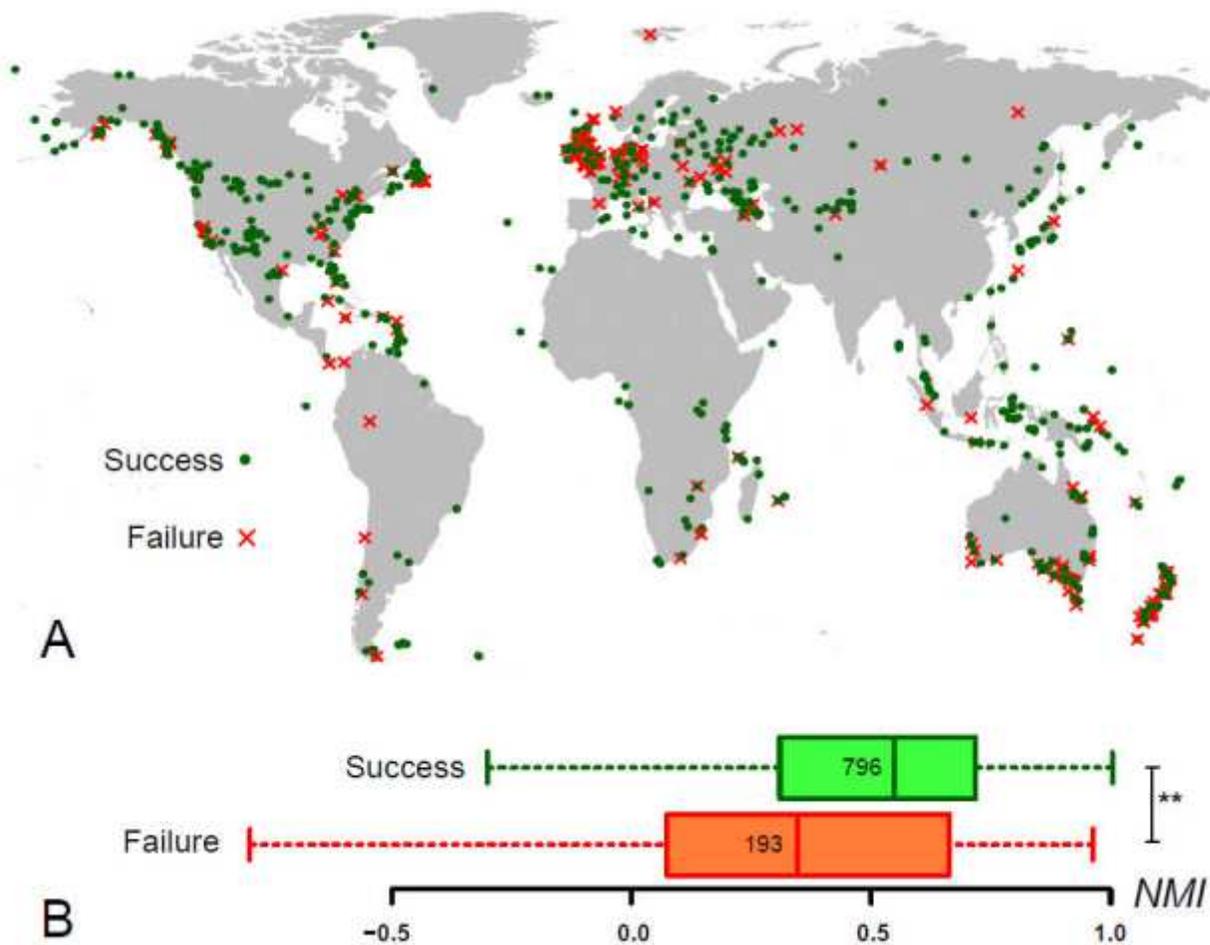


Figure 2

NMI and establishment outcome. (A) spatial distribution of successful and failed introductions. (B) NMI is significantly higher in successful establishments. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

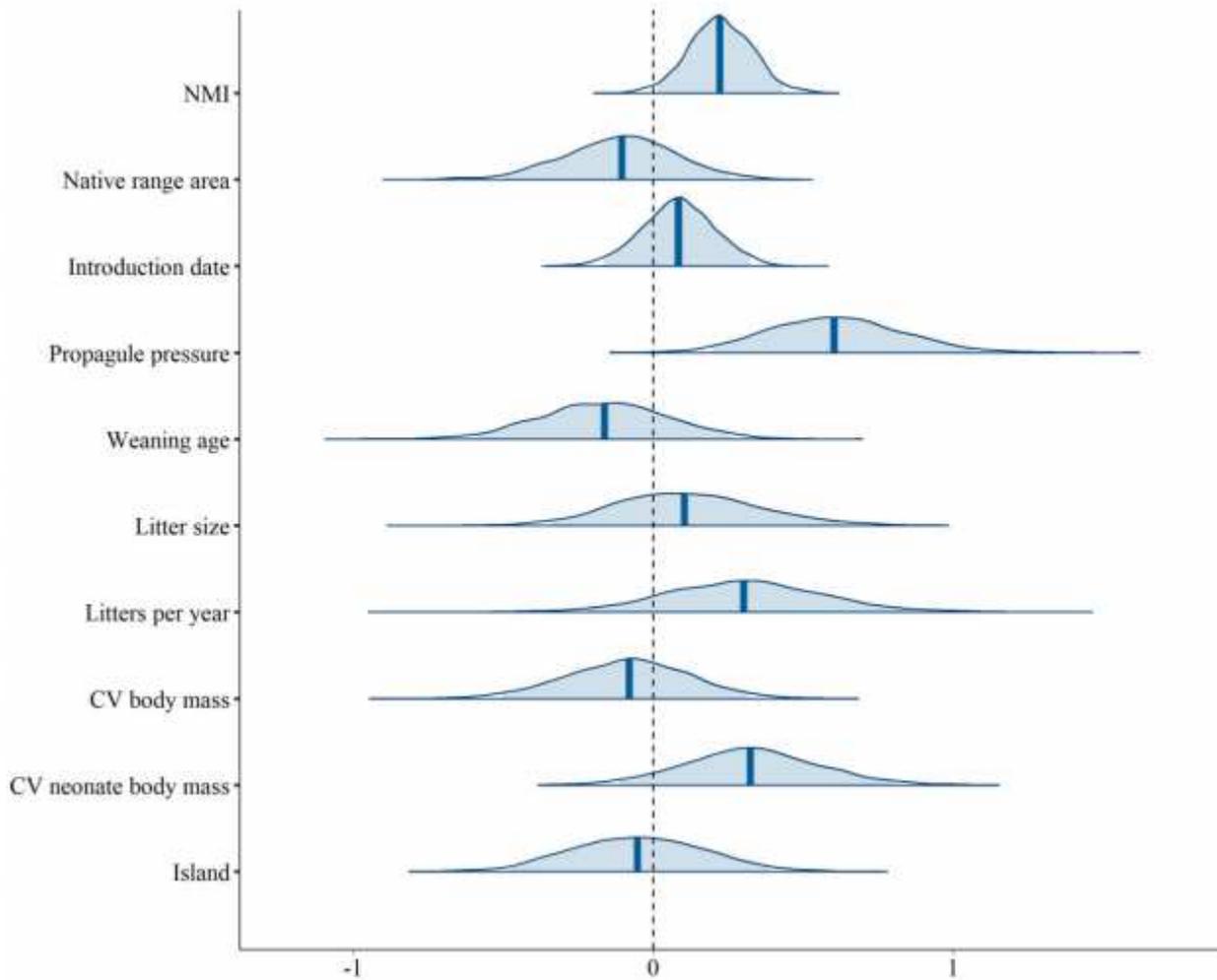


Figure 3

Posterior coefficient estimates of the Bayesian model. Distribution of coefficients for fixed effects are shown. Vertical blue lines represent the median of the posterior distribution of effects (i.e. the strength of effect), while the blue shaded areas under the curves represent the 95% HPD intervals. The vertical dotted line indicates no effect. The posterior probability for a positive effect of the NMI on establishment success ($P[NMI > 0]$) equals 98.1%.