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Intraspecific Trait Variation Is Correlated with Establishment Success of Alien Mammals

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abstract: Many studies have aimed to identify common predictors of successful introductions of alien species, but the search has had limited success, particularly for animals. Past research focused primarily on mean trait values, even though genetic and phenotypic variation has been shown to play a role in establishment success in plants and some animals (mostly invertebrates). Using a global database describing 511 introduction events representing 97 mammalian species, we show that intraspecific variation in morphological traits is associated with establishment success, even when controlling for the positive effect of propagule pressure. In particular, greater establishment success is associated with more variation in adult body size but, surprisingly, less variation in neonate body size, potentially reflecting distinct trade-offs and constraints that influence population dynamics differently. We find no mean trait descriptors associated with establishment success, although species occupying wider native distribution ranges (which likely have larger niches) are more successful. Our results emphasize the importance of explicitly considering intraspecific variation to predict establishment success in animal species and generally to understand population dynamics. This understanding might improve management of alien species and increase the success of intentional releases, for example, for biocontrol or reintroductions.

Keywords: alien species, biological invasions, coefficient of variation, invasive species, plasticity hypothesis, trait variation.

Introduction

Research on alien species advances our knowledge of many biological phenomena, including ecological interactions, evolutionary relationships, and biogeographic processes (Sax et al. 2005). Moreover, some established alien species become invasive and have substantial ecological and socioeconomic impacts (Pimentel et al. 2005; Kettunen et al. 2008; Vilà et al. 2009; Kumschick and Nentwig 2010). For these reasons, numerous researchers have tried to identify species' traits and factors that correlate with the establishment and invasion success of alien species that were introduced in the past, hoping that this information can be used to predict the establishment and invasion success of alien species that will be introduced in the future (Lockwood et al. 2005; Jeschke and Strayer 2006; Davidson et al. 2011; Kumschick et al. 2013). If this goal can be achieved, we will better understand what drives biological invasions and other ecological phenomena (e.g., natural range expansions), and, importantly, we could prevent the potential negative impacts of future invaders.

The search for common traits or factors that correlate with establishment and/or invasion success has had mixed success thus far. The only factor that has been consistently correlated with establishment and invasion success across diverse taxonomic groups and regions is propagule pressure, that is, the number of individuals introduced and the frequency of introductions (Lockwood et al. 2005, 2009; Sol et al. 2005, 2008; Jeschke and Strayer 2006; Simberloff 2009; Keller et al. 2011; Rossinelli and Bacher 2015). Additional factors and traits appear to be relevant for some groups. For example, in plants, invasive species exhibit greater growth rates and produce more leaves and shoots than noninvasives (van Kleunen et al. 2010). Larger seeds and herbivore resistance are also determinants of establishment success in plants (Kempel et al. 2013). In animals, specialized parasitic wasps have higher establishment success (Rossinelli and Bacher 2015), while among birds, Sol et al. (2012) found that successful invaders are characterized by life-history strategies that give priority to fu-

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ture rather than current reproduction. Finally, relative brain size has been correlated with establishment success in birds and mammals, possibly because species with relatively larger brains exhibit more flexible behavior, allowing them to cope better with novel environments (Sol and Lefebvre 2000; Sol et al. 2008, 2012; but see Jeschke and Strayer 2006).

The population biology literature has shown that variation among individuals and/or populations within a species can influence population dynamics (Filin and Ovadia 2007; González-Suárez et al. 2011). The plant invasion biology literature has paid considerable attention to one type of variation formulating the phenotypic plasticity hypothesis, which posits that phenotypically plastic species are better able to establish and spread in novel environments (Richards et al. 2006; Davidson et al. 2011). Several experimental and observational studies have compared native and alien/invasive plants, but their results offer mixed support for this hypothesis, including higher plasticity in invasives, no differences, and even higher plasticity in natives (Funk 2008; Davidson et al. 2011; Godoy et al. 2011; Palacio-López and Gianoli 2011; Paquette et al. 2012). On the other hand, the majority of animal studies looking for determinants of alien species' establishment success has focused on the role of abiotic factors and/or mean trait values of the studied species without explicitly accounting for intraspecific trait variation (Duncan et al. 2003; Forsyth et al. 2004; Hayes and Barry 2008). Those studies that have explored the role of variation in animals have focused on single alien species (Dybdahl and Kane 2005; Engel et al. 2011; Knop and Reusser 2012; Zalewski and Bartoszewicz 2012), likely because capturing intraspecific variation requires additional research and data compilation efforts, which have limited the availability of variation estimates for comparative studies. The exception is a very recent meta-analysis that shows invasive species (including plants, invertebrates, and one fish) exhibit higher genetic and phenotypic variation than noninvasive species (Forsman 2014). However, the potential role of intraspecific variation as a determinant of establishment success of terrestrial vertebrates remains unexplored.

In conservation biology, many comparative analyses have looked for determinants of species' threat status, trying to identify traits and factors that make species more vulnerable to extinction (Purvis et al. 2000; Cardillo et al. 2005; Davidson et al. 2009; González-Suárez et al. 2013). In this context, González-Suárez and Revilla (2013) recently showed that mammals with low intraspecific variation in diverse intrinsic traits are particularly vulnerable to extinction. An intuitive explanation for this result is that species with low variation have a reduced capacity to respond to occurring threats—such as land use or climate change—than species with high variation. Within-species variation

in life history (e.g., age at sexual maturity), morphology (e.g., adult body size), or ecological traits (e.g., home range size or group size) can provide flexibility in response, which can reduce risk of extinction and may favor establishment and expansion of alien species. Additionally, species with high intraspecific trait variation may also be better able to establish in novel environments because diverse individuals are potentially preadapted to a wider range of environmental conditions. Indeed, experimental data show that more variable founder groups are more likely to successfully establish in novel natural environments (Forsman 2014). Finally, although variation can be beneficial, it should be noted that not all variation must necessarily lead to increased establishment success or persistence (Robinson et al. 2013). Variation in some traits might be neutral (e.g., eye color) or even lead to lower establishment success if this variation decreases fitness (e.g., traits associated with asymmetry; Møller and Swaddle 1997). In this study, we use a comprehensive global data set of mammalian introductions to explore for the first time the role of intraspecific variation and mean trait descriptors in establishment success of alien mammals.

Methods

Data

We compiled a global database of human-mediated introductions of mammals to new locations, drawn largely from Long (2003) and references therein. The introduction of a species to a new location in the wild (an introduction event) was defined as the release of individuals of a species to an island or a governmental state within a continental mainland that is outside the species' current native range. We considered an introduction as successful if it resulted in the establishment of a persistent population on the island or state where the species was introduced, and unsuccessful otherwise. We excluded recent introductions (i.e., those that took place after 1985)—for which it may be too early to determine whether a viable population has been established—and introductions for which the outcome (success or failure) was uncertain. Because the number of released individuals is a major determinant of establishment success (Lockwood et al. 2005), we restricted our analyses to introduction events for which data on introduction effort were available. For multiple releases of the same species to the same location within time intervals <20 years, the total number of individuals released was pooled and considered as a single release. Subsequent introductions of species that were already established in an area were discarded. Most releases were intentional, except for 31 accidental escapes and seven observations (all of *Canis latrans*) in which the type of re-

lease was unknown. A previous analyses of this data set shows that the type of release did not influence establishment success (Sol et al. 2008).

To estimate intraspecific variation in species' traits for the species for which introduction data were available, we followed the procedure described by González-Suárez and Revilla (2013), using the raw data file from the mammalian life-history data set PanTHERIA (Jones et al. 2009). This file includes 97,827 records describing 4,204 mammalian species recognized by Wilson and Reeder's (2005) mammalian taxonomy. We considered traits in four general categories: morphology, ecology, reproductive timing, and reproductive output (table 1), which we expected a priori could explain differences in establishment success. We calculated the trait's arithmetic mean and coefficient of variation (CV) for each species with more than one record per trait, after excluding records classified as minimum or maximum and making the corrections mentioned by González-Suárez and Revilla (2013) and a few additional corrections made for this study (table A1; tables A1–A5 available online). Estimated CV values reflect variation among estimates reported by different studies (interpopulation variation). Unfortunately, data were not available to estimate intrapopulation variation. After combining both databases (trait and introduction data sets), we had information on 511 introductions representing 97 mammalian species with varying amounts of data per trait (table 1). The compiled data set is available in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.sp963 (González-Suárez et al. 2015).

The described estimates of intraspecific variation (CV) capture diverse sources of variation, including temporal, spatial, and between sexes as indicators of differences among groups and/or populations. However, differences caused by sexual dimorphism not only reflect that individuals from a species can be variable (the variation we are interested in) but also may capture the influence of the distinct life-history strategies of each sex, which could confound our results. To evaluate this potential confounding effect, we estimated sex-specific CVs for traits that may be influenced by sexual dimorphism (table 1). Sex-specific CVs were calculated using only measures obtained from same-sex individuals. The species' CVs were then defined as the average of the female and male CVs, or if data were available for only one sex, we used that within-sex CV estimate (which does not include any variation due to dimorphism). Because many trait records in PanTHERIA provide information from both sexes combined or the sex of the measured individuals is unspecified in the study, sex-specific CVs could not be estimated for several of the species for which CVs were originally obtained (table 1). Therefore, we completed all analyses on the basis of general CVs for which more data were available but then repeated the analyses using available sex-specific CVs to evaluate whether our findings were confounded by sexual dimorphism.

Data Analyses

The general modeling procedure followed recommendations in Duncan et al. (2014). We modeled establishment success as a binary response using generalized linear mixed models (GLMMs) fitted with the procedure glmer from the package lme4 (ver. 1.0-6; Bates et al. 2014) in R 3.1.1 (R Core Team 2014), assuming a binomial error distribution and logit link function. To relate to previous studies that focused on mean trait values, our models considered both mean and CV for the diverse traits proposed. In addition, because species that have wider habitat breadths and occupy wider (native) distribution range areas may also exhibit more variation and could have a wider potential niche that facilitates their establishment, we also consider whether native range area and habitat breadth influence establishment success in addition to any identified relevant traits. The native range area was estimated with International Union for Conservation of Nature spatial data (IUCN 2013), using only polygons defined as native or reintroduced origin and extant or probably extant presence with a cylindrical equal area projection. Habitat breadth was estimated by the number of distinct terrestrial ecoregions (updated map available from the World Wildlife Fund; Olson et al. 2001) that overlapped with these

Table 1: Available sample size for each of the species' traits from the database PanTHERIA considered in this study

Trait	N	$N_{\text{sex specific}}$
Morphology:		
Adult body mass	92	64
Neonate body mass	74	19
Ecological traits:		
Home range size	52	25
Population density	49	NM
Group size	24	5
Reproductive timing:		
Litters per year	60	NM
Weaning age	71	2
Sexual maturity age	76	65
Reproductive output:		
Litter size	89	NM
Gestation length	85	NM

Note: N is the number of species with intraspecific variation data; $N_{\text{sex specific}}$ is the number of species for which we could calculate sex-specific coefficients of variation. For certain traits, sex-specific estimates are not meaningful (NM). For 33 species, we calculated litters per year as 365/interbirth interval (interbirth interval = days between births). Gestation length was calculated excluding the period of delayed implantation (exclusion was based on notes included in the comments column of PanTHERIA or by inference on the basis of other available values).

native range areas. In addition, we also evaluated the importance of introduction event characteristics, including propagule pressure (how many individuals were released/introduced at each event) and the year of introduction. All continuous variables included as fixed effects (except CVs and habitat breadth) were $\log_{10}$ transformed, and all predictors were standardized (subtracting the mean and dividing by the standard deviation) before analyses.

Tested models included the region of introduction (defined as Australian, Nearctic, Oceanic, Palearctic, and Tropical) as a random effect to control for spatial autocorrelation. Models also included taxonomic random effects of species nested within family and order to account for shared evolutionary relationships. We explored whether such a structure of random effects effectively accounted for phylogenetic nonindependence by testing model residuals for evidence of phylogenetic signal (Revell 2010). For this test, we needed a single entry per species, and thus we used equivalent models describing binomial probabilities per species (with the number of introductions that result in establishment and the number of failed introductions as the dependent variables). For these analyses, we used the median number of individuals introduced in all events in which a species was involved as the estimate of propagule pressure. Results from both approaches were qualitatively the same. The residuals of these models were then tested using the procedure phylosig from the package phytools 0.3-72 in R (Revell 2012). The procedure phylosig computes the phylogenetic signal in a variable (in our case, model residuals) estimating Pagel's λ (Pagel 1999) or Blomberg's K (Blomberg et al. 2003).

Unfortunately, missing trait data are prevalent in our database (table 1) and present a challenge for the analyses (González-Suárez et al. 2012). Although imputation techniques may be used to fill missing data, we did not follow this approach because missing values are not missing at random in these data (González-Suárez et al. 2012) and because of the complexity of imputing intraspecific variation. Instead, we used a two-step approach based on variable selection using the Akaike information criterion (AIC_c) and variable weights (Burnham and Anderson 2002) to maximize the use of available data. First, we explored the correlation among variables in each trait category (table 1). To avoid problems with model fitting due to collinearity, from highly correlated pairs of variables (Pearson's $r \geq |0.70|$; Dormann et al. 2013), we selected the variable with the largest sample size, or if sample sizes were similar, we ran separate analyses for each variable. Using a different threshold to identify correlated variables (Pearson's $r \geq |0.60|$ or $r \geq |0.80|$) did not qualitatively change our results (table A2). To evaluate whether this approach effectively addresses any possible collinearity issues, we also estimated variance inflation factors (VIFs) for fitted model.

Using non–highly correlated variables within each general category, we defined all possible model combinations and estimated variable weights, ω (Burnham and Anderson 2002). From each category, we selected variables with $\omega \geq 0.70$ as potentially relevant. Using this selection threshold meant that no variables from a category were identified as potentially relevant if the null model (a model including only random effects and an intercept) was supported (its AIC_c was within two units of the best model). We then defined a new set of models based on all possible combinations of these selected variables, also including habitat breadth, native distribution range area, propagule pressure, and the year of introduction to account for additional sources of variation and introduction event characteristics. The final model was defined with variables identified as possibly relevant ($\omega \geq 0.70$) from this set of models. The relevance of predictors was finally assessed on the basis of estimated effects sizes (standardized model coefficients) and their standard errors. We did not estimate model coefficients using model averaging techniques (Burnham and Anderson 2002) because excluding non-relevant variables often increased the sample size available to fit the model. Overall model fit was evaluated by estimating the classification ability using the nonparametric estimate of the area under the curve of receiver operating characteristic plots (Hosmer and Lemeshow 2000) and two recently proposed R^2 estimates for generalized linear mixed models: R_c^2, which describes the variation explained by both fixed and random factors; and R_m^2, representing the variation explained by the fixed factors only (Nakagawa and Schielzeth 2013). Variable weights and R^2 values were estimated using the procedures model.avg and r.squaredGLMM from the package MuMIn 1.9.13 (Barton 2013) in R.

A potential caveat of our analyses is that the accuracy with which true population CVs can be estimated depends on the sample size available to generate the estimate. In PanTHERIA, the number of records per species per trait varies considerably, which can possibly lead to imprecise CV estimates. We followed González-Suárez and Revilla (2013) and evaluated the robustness of our final results to variation in CV estimates using bootstrapped samples. For each trait in the final model, we generated 2,000 samples per species of n observations each (with replacement), where n is the median number of available records per species for that trait. Using these samples, we calculated CV values based on equal sample sizes (n) for all species, although for species with few observations, the samples included mostly repeated records, since no other information is available. Records for each trait are independent; thus, we had to generate separate bootstrapped samples for each trait, which complicated the use of the bootstrapped values to fit models (there would be 2,000 × 2,000 possible

combinations of the bootstrapped samples for a model with just two traits). Our approach instead was to calculate an arithmetic mean of the 2,000 bootstrapped CVs with a lower and upper 95% confidence interval. We then refitted the final model, replacing the original CV values with the mean and confidence intervals and comparing these results with those based on the original CV estimates.

Results

Introduction data were available for 511 events involving 97 different mammalian species from 12 different orders (fig. A1; figs. A1, A2 available online). The most commonly introduced mammals were artiodactyls, rodents, and carnivores (with 32, 18, and 16 species introduced in 206, 113, and 97 events, respectively). Of the 511 events, 390 (76.3%) representing 84 species resulted in established populations, while 121 events (23.7%) representing 53 species did not result in establishment. Although a priori considered to be a potentially relevant ecological trait, group size was not included in the analyses, since data were available for only a few introduced mammals (table 1).

The category analyses showed that the probability of establishing successfully after introduction was influenced by intraspecific variation in morphology but not mean morphological descriptors (table 2). In particular, successful establishment was apparently more likely for mammals that exhibit greater intraspecific variation in adult body mass but less variation in neonate body mass. No mean or CV of ecological or reproduction traits was identified as relevant (table 2). To define the final model, we combined the two identified morphological CVs, habitat breadth, native distribution range area, propagule pressure, and the year of introduction. Because habitat breadth and native range area were highly correlated (Pearson's $r = 0.82$), we defined two possible variable combinations, each including one of these variables. In both combinations, morphological CVs and propagule pressure were identified as relevant, while the year of introduction was always excluded (table 3). When included, native distribution range area was also identified as relevant, whereas our estimate of habitat breadth was not clearly associated with probability of establishment success.

We defined a final model with morphological CVs, propagule pressure, and native range area as predictors (table 3) because a model without range area provided a poorer fit to the data (ΔAIC = 8.36). This final model suggests that successful establishment was associated with greater variation in adult body mass, less variation in neonate body mass, larger native range areas, and greater propagule pressure. The negative effect of variation in neonate body mass was not an artifact of collinearity of this trait with variation in adult body mass (Pearson's $r = 0.52$), since the

Table 2: Results for the category analyses exploring how species' traits predict the probability of success of introduced mammals

Variables	Mean		CV	
	ω	β (SE)	ω	β (SE)
Morphology (453, 74):				
Adult body mass	.37	...	**.78**	.6 (.24)
Neonate body mass	CO	CO	**.82**	−.6 (.23)
Ecological traits (197, 33):				
Combination 1:				
Home range size	.62	...	.44	...
Population density	NA	NA	.28	...
Combination 2:				
Home range size	NA	NA	.50	...
Population density	.33	...	.28	...
Reproductive timing (414, 67):				
Litters per year	CO	CO	CO	CO
Weaning age	.37	...	.29	...
Sexual maturity age	.30	...	.29	...
Reproductive output (487, 84):				
Litter size	.27	...	.34	...
Gestation length	.27	...	.37	...

Note: We report variable weights (ω), with relevant variables ($\omega \geq 0.70$) in bold, and the best estimate of the slope coefficient with its associated standard error (β [SE]) for the final category model. Within each category, we report in parentheses the number of introductions and species introduced used to define variable weights and, if different, the sample size used to fit the final category model. CO indicates a highly correlated variable (Pearson's $r \geq |.70|$) not included in the analyses. Ellipses indicate variables not in the final category model. Variables were standardized for analyses (mean trait values were first $\log_{10}$ transformed). Mean population density and mean home range size are highly correlated (Pearson's $r = -.83$) but have similar sample sizes available; we therefore ran two possible model combinations: combination 1 excluded mean population density, whereas combination 2 excluded mean home range size. NA, not applicable.

negative relationship was also observed in a model that did not include variation in adult body mass (regression coefficient slope $\beta = -0.5$, SE = 0.20). Moreover, we found the same qualitative results when taxonomic orders were analyzed separately and excluding marsupial species for which neonate body mass may be uniquely small (table A3).

The final model had overall good classification ability (area under the curve = 0.81) and explained a substantial amount of the observed variation in the data ($R_c^2 = 0.37$, $R_m^2 = 0.30$). We found no evidence of phylogenetic signal in model residuals from the category or final analyses (all Pagel's $\lambda < 0.01$, $P > .99$; all Blomberg's $K < 0.13$, $P > .41$), indicating that the taxonomic random effects effectively addressed the issue of nonindependence of data points as a result of species' shared evolutionary history. VIF values were <2.5 for all fitted models (VIF < 1.9 for the final model), suggesting low collinearity among predictors.

Table 3: Results for the combined model exploring how species' traits and introduction event characteristics predict the probability of establishment success in mammalian introductions

Variables	ω_{comb1}	ω_{comb2}	β (SE)
CV adult body mass	**.93**	**.80**	.6 (.19)
CV neonate body mass	**.98**	**.82**	−.8 (.21)
Native distribution range area	**.99**	NA	.5 (.15)
Habitat breadth	NA	.52	…
Propagule pressure	**1.00**	**1.00**	.8 (.18)
Year of introduction	.44	.33	…

Note: We report variable weights (ω), with relevant variables ($\omega \geq 0.70$) in bold, and the best estimate of the slope coefficient and its associated standard error (β [SE]) for a final model fitted considering only the final relevant variables. Weights were estimated on the basis of 428 introduction events from 70 mammalian species. The final model was fitted for 441 introductions of 72 species. All independent variables were $\log_{10}$ transformed (except coefficients of variation [CVs] and habitat breadth) and standardized for analyses. Ellipses indicate variables not in the final model. Native distribution range area and habitat breadth are highly correlated (Pearson's $r = 0.82$); therefore, we analyzed two possible model combinations: combination 1 excluded habitat breadth, whereas combination 2 excluded native range area.

We used the final model (with unstandardized coefficients) to make predictions for the observed range of values of each trait, fixing other variables to their median value across species except for propagule pressure, for which we set three different levels (fig. 1). Introductions with high propagule pressure (1,000 introduced individuals) were predicted to result in an established population in most cases, with minor effects of intraspecific variation or range size. For lower propagule pressure (<100 introduced individuals), however, the expected probability of establishment could vary significantly, depending on the level of intraspecific variation in adult body mass, neonate body mass, and the native distribution range area (fig. 1). For example, a species with little variation in body mass (e.g., the arctic hare *Lepus arcticus*; $CV_{adult\,body\,mass} = 0.04$) was predicted to establish a population in about 33% of introductions of 10 individuals (the observed success was 45%, five out of 11 attempts, with a median of 17 released individuals). On the other hand, a species with high variation (e.g., the sika deer *Cervus nippon*; $CV_{adult\,body\,mass} = 0.58$) was predicted to establish a population in about 88% of introductions of 10 individuals (observed success was 82%, nine out of 11 attempts, with a median of seven released individuals). Importantly, intraspecific variation would appear to have been relevant for many of the 511 introduction events we studied, since there were <100 introduced individuals for 414 of these events (median propagule pressure for all introductions is 18; fig. A2).

Our results were qualitatively the same using available sex-specific CV estimates (table A4), including the effect of the variation in adult body size (a trait in which the influence of sexual dimorphism could be particularly strong). We did not have sufficient data to estimate sex-specific variation for neonate body size for many species. Although this trait can also be affected by sexual size dimorphism (but less so than adult mass; Badyaev 2002), for the 19 species with data, sex-specific $CV_{neonate\,body\,mass}$ were well correlated with the general $CV_{neonate\,body\,mass}$ used in the analyses (Pearson's $r = 0.61$). Interestingly, for some dimorphic species, we found that the high variation in adult body size estimated on the basis of all data was also detectable within sexes. For example, we found high variation in adult body size of the sika deer ($CV_{adult\,body\,mass} = 0.58$, on the basis of 15 records), yet this variation was not due to sexual dimorphism, since the estimate of within-male variation was similarly high ($CV_{male\,adult\,body\,mass} = 0.53$, on
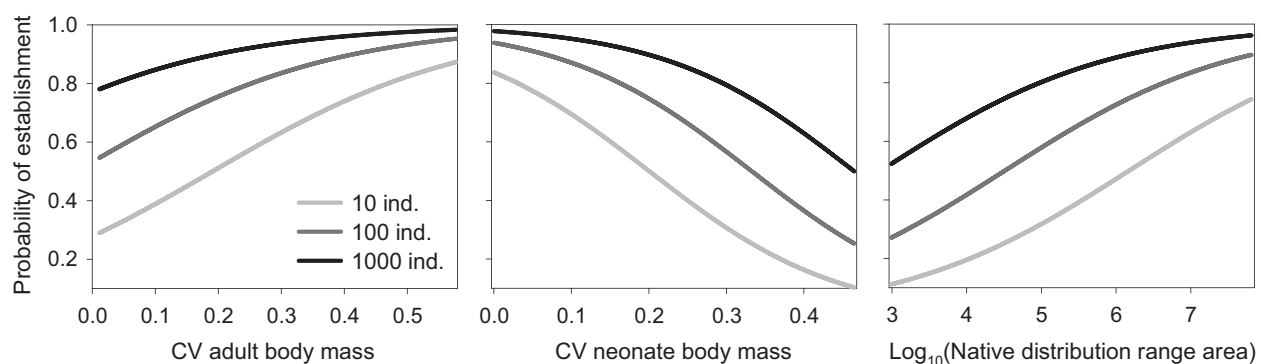
Figure 1: Predicted probability of establishment success as a function of different levels of intraspecific morphological trait variation and the native distribution range area. Predictions are based on the final model and were obtained by exploring the range of observed values for a given variable while setting other trait variables to their median observed value. For propagule pressure, we considered three distinct levels reflecting a range of observed numbers of introduced individuals (ind) in the 511 events analyzed (fig. A2, available online). CV, coefficient of variation.

the basis of 11 records describing only adult males; there was a single estimate of adult female body size; thus, no $CV_{\text{female adult body mass}}$ could be calculated). Similarly, for the red deer *Cervus elaphus*, we estimated $CV_{\text{adult body mass}} = 0.47$, on the basis of 29 records, yet males appeared to actually be more variable ($CV_{\text{male adult body mass}} = 0.53$, from 14 records) while females may be more similar (but still quite variable; $CV_{\text{female adult body mass}} = 0.26$, from four records). In other species, such as the Barbary sheep *Ammotragus lervia*, much of the variation in adult body size did result from sexual dimorphism ($CV_{\text{adult body mass}} = 0.41$, $CV_{\text{male adult body mass}} = 0.12$, $CV_{\text{female adult body mass}} = 0.18$). Nevertheless, our general findings were not affected by these changes, and we can conclude that variation in adult body size (overall or within sex) is correlated with greater establishment success. The identified relationships between morphological intraspecific variation and establishment success in the final model results were also generally robust to variation in CV estimates (table A5 shows the model coefficients calculated with bootstrapped CV estimates).

Discussion

Our results show that intraspecific variation in morphological traits, propagule pressure, and the native distribution range area can be strong predictors of establishment success in alien mammal introductions. On the other hand, variation in ecological and reproductive traits was apparently not associated with success, possibly reflecting data limitation (estimates of ecological trait variation were available for only approximately one-third of the studied species) or the fact that some sources of variation may not play key roles in determining establishment success. It should be noted that we lacked variation in potentially relevant ecological traits, such as diet breadth or physiological tolerance (Higgins and Richardson 2014). In our analyses, variation in these traits may be indirectly captured by the proxy variable native distribution range area, since species occupying larger ranges are likely to have broader physiological tolerances and be exposed to (and use) more diverse food resources. Interestingly, we found that mean trait values were relatively unimportant. In fact, our analyses did not support any influence of mean values, suggesting a possible explanation for why some previous studies of mammalian introductions (Jeschke and Strayer 2006; Sol et al. 2008), which considered only means, may have failed to identify species' traits as good predictors of establishment success.

A mean trait that is regularly associated with establishment success in vertebrates is relative brain size, which can be associated with behavioral flexibility. Sol et al. (2008) analyzed the same mammalian introduction database we used and found that relatively larger brains are associated with greater establishment success in alien mammals. However, these authors did not explore the role of intraspecific trait variation, although they did consider other mean trait values (e.g., body mass, fecundity). We refitted our final model, including relative brain size estimated using taxonomically adjusted brain residuals: residuals of regression lines of log-transformed brain mass on log-transformed body mass defined for each taxonomic order (provided in table A1 of Sol et al. 2008). In this model, relative brain size was not associated with establishment success ($\beta = 0.2$, $SE = 0.19$; data were available for 402 events representing 55 species) once we accounted for the major effects of morphological variation ($CV_{\text{adult body mass}}$: $\beta = 0.8$, $SE = 0.23$; $CV_{\text{neonate body mass}}$: $\beta = -1.1$, $SE = 0.25$), native distribution range area ($\beta = 0.6$, $SE = 0.18$), and propagule pressure ($\beta = 0.7$, $SE = 0.19$; model VIFs < 2.2). Brain size is often interpreted as a measure of behavioral flexibility leading to diversity of responses to novel conditions (Sol et al. 2005, 2008). This diversity of responses or flexibility is also the proposed mechanism by which within-species trait variation could benefit alien species; for the subset of species tested in our study, direct estimates of variation in adult body mass and native distribution range area appear to capture this flexibility better than relative brain size. It would be interesting to evaluate whether this finding is particular to the subset of species analyzed or is consistent across mammals and other vertebrates.

Variation in some traits can be important because it reflects greater flexibility to new and/or fluctuating environmental conditions. Indeed, our results show that mammalian introductions were more likely to lead to establishment if the introduced species exhibited greater intraspecific variation in adult body mass and had wider native distribution range areas. Variation in adult body size can lead to more flexibility by changing foraging requirements (targeting different prey sizes) or territorial/mating strategies. Interestingly, we also found that less variation in neonate body mass was associated with increased probability of establishment success. As mentioned in the introduction, not all sources of observed intraspecific variation may be adaptive in novel environments, where conditions may deviate from the species' optimum. For example, an experimental study in plants found reduced phenotypic plasticity in some traits (e.g., nitrogen content) among invasive species compared with native congeners (Godoy et al. 2011). Increased variation in neonate size may indicate a reduced ability in pregnant females to buffer their offspring against unfavorable environmental conditions (Gaillard et al. 2000). Neonate size influences early survival, with smaller neonates having lower survival probability (Clutton-Brock et al. 1987; Loison et al. 1999), so species in which neonate size is more variable (more dependent

on environmental conditions) could have increased variation in juvenile survival that may lead to increased vulnerability to extinction and lower probability of establishment (Vindenes et al. 2008). While the actual mechanisms by which neonate variation influences establishment success remain unknown for the moment, our findings suggest that the variation observed in body size at different stages may actually reflect different environmental and life-history trade-offs, some of which result in variation that is advantageous for establishing populations in novel environments while others apparently do not.

Model predictions from our analyses suggest that intraspecific morphological variation was particularly relevant for introductions of <100 individuals, which were in fact the most common in mammals. In birds, most introductions also comprise small numbers of individuals released (Blackburn et al. 2009). Therefore, morphological intraspecific variation could play a role in the establishment success of the majority of introductions of alien mammals and possibly other vertebrates. If hundreds of individuals are introduced into an area at once, their intrinsic characteristics may be mostly irrelevant, yet when few individuals are released, intraspecific variation can be critical. In fact, the establishment success of diverse populations of the same species can also be influenced by the variation among individuals within the founder group. In an experimental study, Forsman et al. (2012) found that same-size founder groups of pygmy grasshoppers (*Tetrix subulata*) that included more dissimilar individuals (more variable groups) were more likely to establish successfully in novel habitats than more homogeneous groups.

Although ecologists have long been interested in the role of intraspecific variation for population and community dynamics (Bolnick et al. 2011), most studies have been theoretical or focused on particular populations (e.g., Filin and Ovadia 2007; Vindenes et al. 2008; González-Suárez et al. 2011). This study takes a different approach to this question, using global comparative analyses. Our findings, together with those of González-Suárez and Revilla (2013), emphasize the importance of considering intraspecific variation for inferring population dynamics—particularly at small population sizes—and reveal the role of trait variation as a determinant of establishment success and extinction risk. These results might also partly explain the largely unsuccessful search for general predictors of establishment success thus far, since past studies focused on mean traits (Hayes and Barry 2008). Future work is necessary to determine whether our results can be generalized to other taxonomic groups and to understand how different processes leading to observed variation influence population dynamics. To achieve this goal, it is critical to assemble data sets that capture intraspecific variation—if possible at the population level—instead of providing only mean trait descriptors, while trying to avoid taxonomic and spatial biases that can influence results from comparative analyses (González-Suárez et al. 2012). In addition, future research should aim to identify the mechanisms responsible for the observed patterns, differentiating genetic and phenotypic sources of variation, since they may play different roles in population dynamics. Finally, our results could have implications for conservation management and control of alien species. They suggest that reintroduction efforts are more likely to be successful for species with greater intraspecific variation in adult body mass, less variation in neonate body mass, and wider native distribution range area, offering a possible simple rule of thumb for allocating limited resources to manage species of conservation concern. Also, our model can be helpful to identify species more likely to establish once introduced and thus to outline preemptive measures for particularly risky species in order to avoid their introduction into susceptible areas.

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