

Determinants of vertebrate invasion success in Europe and North America

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Abstract

Species that are frequently introduced to an exotic range have a high potential of becoming invasive. Besides propagule pressure, however, no other generally strong determinant of invasion success is known. Although evidence has accumulated that human affiliates (domesticates, pets, human commensals) also have high invasion success, existing studies do not distinguish whether this success can be completely explained by or is partly independent of propagule pressure. Here, we analyze both factors independently, propagule pressure and human affiliation. We also consider a third factor directly related to humans, hunting, and 17 traits on each species' population size and extent, diet, body size, and life history. Our dataset includes all 2362 freshwater fish, mammals, and birds native to Europe or North America. In contrast to most previous studies, we look at the complete invasion process consisting of (1) introduction, (2) establishment, and (3) spread. In this way, we not only consider which of the introduced species became invasive but also which species were introduced. Of the 20 factors tested, propagule pressure and human affiliation were the two strongest determinants of invasion success across all taxa and steps. This was true for multivariate analyses that account for intercorrelations among variables as well as univariate analyses, suggesting that human affiliation influenced invasion success independently of propagule pressure. Some factors affected the different steps of the invasion process antagonistically. For example, game species were much more likely to be introduced to an exotic continent than nonhunted species but tended to be less likely to establish themselves and spread. Such antagonistic effects show the importance of considering the complete invasion process.

Keywords: aliens, establishment, exotics, introduction, invasion, naturalized species, nonindigenous species, nonnative species, sexual dimorphism, spread

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Introduction

Much effort is being devoted to controlling invasive species, because they cause enormous ecological and economic costs and are an important threat to biodiversity (Wilson, 1992; US Congress, 1993; Pimentel *et al.*, 2005). We recently showed that effective barriers against inadvertent species introductions would be very important for the control of invasives (Jeschke & Strayer, 2005). Ideally, such barriers should block high-risk

species but allow entry of species with a negligible risk of becoming invasive. Unfortunately, although scientists have been looking for correlates of invasion success since the 19th century (Gray, 1879; Henslow, 1879), which led to successful predictive models in some taxonomic groups (Rejmánek & Richardson, 1996; Reichard & Hamilton, 1997; Kolar & Lodge, 2002), it is usually difficult to predict which species will become invasive in the new environment. The only factor that is currently agreed upon to be a general determinant of invasion success is propagule pressure (Lockwood *et al.*, 2005). Indication for the influence of such factors as body mass, different life-history traits, or population density has been equivocal (Kolar & Lodge, 2001; Fisher & Owens, 2004). For another factor, affiliation with humans, evidence has recently accumulated that it

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correlates to invasion success (Lockwood, 1999; Rahel, 2000; Blackburn & Duncan, 2001b; Prinzing *et al.*, 2002; Cassey *et al.*, 2004b; Marchetti *et al.*, 2004; Semmens *et al.*, 2004; Taylor & Irwin, 2004; Alcaraz *et al.*, 2005; Ruesink, 2005). However, existing studies do not distinguish whether this correlation is caused only by human affiliates having a higher propagule pressure or whether their affiliation with humans also increases invasion success independently of propagule pressure.

Here, we use a large dataset on vertebrate exchanges between Europe and North America to simultaneously assess the importance of propagule pressure and human affiliation, but also hunting and 17 biological traits that characterize each species' population size and extent (three variables: population density, latitudinal range, native continent), diet (two variables: carnivory as opposed to herbivory, diet breadth), body size (three variables: body mass, body length, relative brain mass), and life history (nine variables: fecundity, offspring size, litter or clutch mass, number of litters or clutches per year, number of offspring per year, degree of parental care, age of first reproduction, maximum lifespan, sexual dimorphism).

We ask two specific questions: (A) Which of these 20 factors are good predictors of invasion success for vertebrates in Europe and North America? Note that we use the term *predictor* in a broad sense, reflecting a correlation derived from comparison rather than an experimentally tested cause. We define a successful invader as a species that completed the three steps of the invasion process: introduction, establishment, and spread (Kolar & Lodge, 2001). Thus, we call a species invasive if it was introduced from Europe to North America or vice versa, if it has established one or more self-sustaining populations in the wild in the exotic continent, and if it spreads substantially from its point of introduction. (B) Do any of the 20 factors affect the different steps of the invasion process antagonistically? That is, do factors that favor success at the first step (introduction) hinder success at the second and third steps (establishment and spread) or vice versa? In pilot analyses of the dataset, we found that the second and third steps were affected by similar factors, so we combined them into a single step in our analyses (cf. Cassey *et al.*, 2004a).

Material and methods

Our study includes all freshwater fish, mammals, and birds that are native to either Europe or North America. We followed the usual geographical definition of Europe, but defined North America as Canada and the United States except Hawaii. Species that are native to both continents were excluded, leaving 2362 species

which were also analyzed by Jeschke & Strayer (2005) who provided detailed information on the number of introduced, established, and invasive species in each taxon and continent. For each species and trait, we extracted data from the literature. The complete list of our sources and the final dataset are freely available from us upon request or online at www.jeschke.tk.

The 20 variables

The details on each of the 20 traits are as follows (references indicate studies that previously analyzed or reviewed the importance of a trait for invasion success of animals or plants). As an index of propagule pressure, we used the number of countries (Europe) or states and provinces (North America) where a species was separately introduced; more exact data on propagule pressure were not consistently available (Veltman *et al.*, 1996; Cassey *et al.*, 2004c, 2005; Forsyth *et al.*, 2004; Marchetti *et al.*, 2004; Sol *et al.*, 2005; reviewed by Kolar & Lodge, 2001; Fisher & Owens, 2004; Lockwood *et al.*, 2005). We defined human affiliation as living in close association with humans. More specifically, human affiliates include domestic animals; other species deliberately raised for pets, food, or sport in large numbers; and species that reach high population densities in human settlements (e.g. rats or house sparrows). Previous studies that analyzed human affiliation as a potential predictor of invasion success are Prinzing *et al.* (2002), Cassey *et al.* (2004b), Semmens *et al.* (2004), Alcaraz *et al.* (2005), and Ruesink (2005). The third trait directly associated with humans was hunting (Alcaraz *et al.*, 2005). We defined game species as those that are deliberately sought for and harvested from the wild in substantial numbers, whether for sport, individual consumption, or commercial harvest. Species that are taken incidentally were not considered as hunted. We included three variables on population size and extent, population density (reviewed by Ehrlich, 1989; data for fish were not sufficiently available to use), latitudinal range in the native continent (Reichard & Hamilton, 1997; Starfinger, 1998; Blackburn & Duncan, 2001a; Cassey, 2002; Prinzing *et al.*, 2002; Cassey *et al.*, 2004b, c; Forsyth *et al.*, 2004; Marchetti *et al.*, 2004; Alcaraz *et al.*, 2005; reviewed by Ehrlich, 1989; Rapoport, 2000; Kolar & Lodge, 2001; Fisher & Owens, 2004), and the native continent (Europe or North America). This last variable is relevant to the imperialism dogma that 'Eurasian species are at an advantage everywhere' (Simberloff, 2004; see also Crosby, 1986; Kolar & Lodge, 2001; Jeschke & Strayer, 2005) and the resistance hypothesis that the less disturbed and richer North American biota offers more resistance against invaders than the European biota (Elton, 1958; Starfinger, 1998; Levine &

D'Antonio, 1999; Mack *et al.*, 2000; Cox, 2004; Zavaleta & Hulvey, 2004; Jeschke & Strayer, 2005; Stachowicz & Tilman, 2005). The two variables on diet were carnivory as opposed to herbivory (reviewed by Kolar & Lodge, 2001; Fisher & Owens, 2004; not available for fish) and diet breadth which we quantified as the number of the following nine different food types included in the diet: nectar, pollen, gum, flowers; fruits, mushrooms; grain, seeds; grass, herbs; leaves, shoots, branches, bark, roots, tubers; detritus; microorganisms not found on detritus (bacteria, hyphae, algae, protozoans, microorganic metazoans); macroorganic invertebrates; vertebrates (McLain *et al.*, 1999; Cassey, 2002; Kolar & Lodge, 2002; Cassey *et al.*, 2004b, c; reviewed by Ehrlich, 1989; Kolar & Lodge, 2001; dietary data not available for fish). We had three variables on body size, adult body mass and length (Cassey, 2002; Roy *et al.*, 2002; Cassey *et al.*, 2004b, c; Forsyth *et al.*, 2004; Marchetti *et al.*, 2004; Alcaraz *et al.*, 2005; Ruesink, 2005; Vila-Gispert *et al.*, 2005; reviewed by Ehrlich, 1989; Kolar & Lodge, 2001; Fisher & Owens, 2004) plus relative brain mass of adults, calculated as the residual of linear regressions of \log_{10} -transformed adult brain masses vs. \log_{10} -transformed adult body masses (Sol & Lefebvre, 2000; Sol *et al.*, 2002, 2005). We did this calculation separately for mammals ($r^2 = 0.98$, constant \pm SE = -0.87 ± 0.022 , slope \pm SE = 0.56 ± 0.010 , $F_{1,75} = 1697$, $P < 0.001$) and birds ($r^2 = 0.89$, constant \pm SE = -1.12 ± 0.066 , slope \pm SE = 0.70 ± 0.017 , $F_{1,354} = 2879$, $P < 0.001$); brain data were not sufficiently available for fish. Finally, our nine life-history variables were fecundity (clutch or litter size; Marchetti *et al.*, 2004; Alcaraz *et al.*, 2005; Vila-Gispert *et al.*, 2005; reviewed by Kolar & Lodge, 2001), offspring size (egg diameter, birth mass, or egg mass for fish, mammals, and birds, respectively; Reichard & Hamilton, 1997; Vila-Gispert *et al.*, 2005; reviewed by Kolar & Lodge, 2001), litter or clutch mass (reviewed by Kolar & Lodge, 2001; no data for fish), number of litters or clutches per year (Vila-Gispert *et al.*, 2005; reviewed by Kolar & Lodge, 2001), number of offspring per year (Cassey *et al.*, 2004b, c; Forsyth *et al.*, 2004; reviewed by Kolar & Lodge, 2001), degree of parental care (Cassey *et al.*, 2004b; Forsyth *et al.*, 2004; Marchetti *et al.*, 2004; Vila-Gispert *et al.*, 2005; an ordinal variable in case of fish (0 = no parental care, 1 = builds nests, 2 = guards eggs, 3 = guards young), weaning age in case of mammals, and age of independence in case of birds), age of first reproduction (Reichard & Hamilton, 1997; Cassey *et al.*, 2004b; Alcaraz *et al.*, 2005; Vila-Gispert *et al.*, 2005; reviewed by Ehrlich, 1989; Kolar & Lodge, 2001), maximum lifespan (Forsyth *et al.*, 2004; Marchetti *et al.*, 2004; Alcaraz *et al.*, 2005; Vila-Gispert *et al.*, 2005; reviewed by Kolar & Lodge, 2001), and sexual dimorphism, defined

as sexual dichromatism according to the human eye or sexual differences in similar secondary sex characteristics such as a mane or antlers, cf. McLain *et al.* (1995, 1999), Sorci *et al.* (1998), Cassey (2002), Cassey *et al.* (2004c), Donze *et al.* (2004), Fisher & Owens (2004); following these studies, we used sexual dimorphism as a conservative indicator for the intensity of sexual selection and did not consider sexual differences in body size because these can reflect differences in the ecological niche occupied rather than the intensity of sexual selection.

Analyses

To answer our questions, we first compared the 20 traits of the species that were introduced from Europe to North America or vice versa with those of species that were not introduced in either direction. For such a comparison, which has previously only been done by Cassey *et al.* (2004a, b), a dataset is needed that includes not only successful but also failed introductions. Because Europe and North America are particularly well-investigated regions and vertebrates are particularly noticeable organisms, we are confident of the high quality of our dataset. Previous estimates suggest that about 16% of the species introductions that actually happened are missing from our dataset, more in fish than in mammals and birds (Jeschke & Strayer, 2005). Our dataset includes both intentional and unintentional introductions. Second, we also compared introduced species that became invasive (i.e. that established themselves and spread) with those that were introduced but did not establish and spread. And third, we combined the first two comparisons and compared the traits of species that became invasive with those that did not. Our analyses include species introductions, establishment, and spread until the end of the 20th century.

For each of the three comparisons and in each taxonomic group (fish, mammals, birds, all species), we performed (A) univariate and (B) multivariate analyses of the data, plus (C) multivariate analyses of phylogenetically independent contrasts. We did the multivariate analyses also for mammals and birds combined (i.e. for the terrestrial species in our dataset). We performed the three analyses as follows.

(A) For univariate analyses, we ran two-tailed binomial tests, U -tests, and t -tests for dichotomous, ordinate, and metric variables, respectively. We did t -tests with \log_{10} -transformed data, if this was necessary to normalize their distribution. We also performed t -tests for unequal variances, if this was necessary. To assess the biological relevance of significant differences revealed by these tests, we additionally calculated effect

sizes d (for more details, see Table 1 and Gurevitch & Hedges, 2001).

(B) For multivariate analyses of the data, we ran stepwise forward (likelihood ratio) logistic regressions with an entry probability of 0.05 and a removal probability of 0.10. Logistic regressions are most appropriate for our dataset, especially because the response variables are binomially distributed (cf. McLain *et al.*, 1995; Cassey *et al.*, 2004a,b; Ruesink, 2005; Sol *et al.*, 2005). Because only those species could be analyzed here for which values of all variables are known, we excluded variables that lacked data for more than 40% of the species and did not have a strong effect on any step of the invasion process in the univariate analyses (i.e. all $|d| < 0.8$ in Table 1, Gurevitch & Hedges, 2001). In this way, we excluded fecundity, clutches per year, offspring per year, age of first reproduction, and sexual dimorphism for fish; population density, brain mass, birth mass, litter mass, parental care, and age of first reproduction for mammals; and population density, brain mass, parental care, and age of first reproduction for birds. For the analyses of birds and mammals combined, we also excluded parental care which was measured differently in each group and, therefore, not comparable. For this analysis, we hence excluded population density, brain mass, offspring mass, litters or clutches per year, parental care, and age of first reproduction. Finally, for the analyses of all species, we additionally excluded variables not available for fish or not comparable among the three taxa, leading to the exclusion of population density, carnivory, diet breadth, brain mass, fecundity, offspring mass, litter or clutch mass, litters or clutches per year, offspring per year, parental care, age of first reproduction, and maximum lifespan.

(C) To correct for phylogenetic dependence in the data, we performed multivariate linear regressions of independent contrasts which were calculated with Mesquite 1.05 and its PDAP module 1.06 (Maddison & Maddison, 2004; Midford *et al.*, 2005). Independent-contrasts analysis is the most established approach for considering phylogenetic dependence in comparative analyses (Felsenstein, 1985; Garland *et al.*, 1992, 1993, 2005; Pagel, 1992; Martins, 1993; Alcaraz *et al.*, 2005). The phylogeny used for the calculations and the underlying sources are freely available from the authors upon request or online at www.jeschke.tk. Branch lengths were arbitrarily set according to Pagel (1992) and diagnostic graphs helped checking assumptions underlying independent-contrasts analysis (cf. Garland *et al.*, 1992, 2005). Following Garland *et al.* (1993) and Martins (1993), we allowed hypothetical ancestors to attain intermediate values of categorical variables. Thus, our response variables were not binomially distributed in this case, which is why we ran linear instead of logistic

regressions. In general, regressions of independent contrasts must be forced through the origin (Garland *et al.*, 1992). We used the same reduced dataset as for the regressions in (B) but \log_{10} -transformed some of the variables before calculating the contrasts to normalize and homogenize the data. We transformed the same variables as for the univariate analyses (Table 1). We again used a stepwise forward method with an entry probability of 0.05 and a removal probability of 0.10.

These three analyses are complementary, each one providing different insights. From (A) to (C), their complexity increases: as multivariate analyses, (B) and (C) take into account intercorrelations between variables, and (C) additionally considers phylogenetic relationships between species. On the other hand, the analyses in (A) covered a larger dataset than the ones in (B) and (C) and were thus more powerful. In fact, they were so powerful that, due to large sample sizes, they often showed significant differences where effect sizes were small. We treat such differences as biologically not very meaningful and consequently do not dwell on them in the 'Results' and the 'Discussion'. In the following, we focus instead on variables with significant tests *and* large effect sizes.

Results

Association with humans

All three analyses showed that association with humans is a strong determinant of vertebrate invasion success (Tables 1–3, Fig. 1). All of the three variables included in this group (propagule pressure, human affiliation, hunting) were positively correlated to invasion success in fish, mammals, and birds. Propagule pressure and human affiliation were, in this order, the two individual strongest determinants of invasiveness across taxa. Information on propagule pressure was available for 128 of the 139 introduced species: on average, they were introduced to 7.5 ± 1.20 (SE) countries, states, or provinces. Human affiliation was a stronger determinant in mammals and birds than in fish. The proportion of human affiliates was 4.0% in fish, 14.3% in mammals, 6.3% in birds, and 7.2% in all species. For propagule pressure and human affiliation, the positive correlations to invasion success held true for the first step of the invasion process (introduction), as well as for the second and third steps combined (establishment and spread). In other words, both variables affected the different steps of the invasion process synergistically. As expected, propagule pressure and human affiliation were correlated to each other (fish: $r_{sp} = 0.29$; mammals: $r_{sp} = 0.28$; birds: $r_{sp} = 0.29$; all species: $r_{sp} = 0.26$; all $P < 0.001$, one tailed). Hence, human affiliates were

Table 1 Results of univariate analyses

Variable	Which species are introduced?					Of the introduced species, which are invasive?					Of all species, which are invasive?				
	Fish (N ≤ 933)	Mammals (N ≤ 549)	Birds (N ≤ 880)	All (N ≤ 2362)	All (N ≤ 2362)	Fish (N ≤ 49)	Mammals (N ≤ 22)	Birds (N ≤ 68)	All (N ≤ 139)	All (N ≤ 139)	Fish (N ≤ 933)	Mammals (N ≤ 549)	Birds (N ≤ 880)	All (N ≤ 2362)	
(A) Association with humans															
Propagule pressure	N/A	N/A	N/A	N/A	N/A	0.68	0.62	1.45	0.92**	0.92**	4.62**	5.39*	6.47*	5.20***	
Human affiliation	1.37***	1.57***	1.10***	1.14***	-0.39	1.80**	1.08*	1.08*	0.60*	0.60*	0.71	2.34***	2.70***	1.88***	
Hunting	1.46***	1.34***	1.17***	1.31***	-0.57	-0.74	0.32	0.32	-0.20	-0.20	0.99**	0.93*	1.40***	1.07***	
(B) Population size and extent															
Population density	No data	-0.31	0.18	-0.15**	No data	No data	0.13	-0.01	0.36	0.36	No data	-0.28	0.17	-0.07	
Native latitudinal range	1.91***	1.58***	0.73***	1.19***	-0.38	0.32	0.35	0.14	0.14	0.14	1.51***	1.71***	0.94**	1.20***	
Native continent Europe [†]	0.14	0.45*	0.39**	0.34**	0.02	0.12	0.50	0.14	0.14	0.14	0.14	0.52	0.79**	0.42*	
(C) Diet															
Carnivory	No data	-0.57**	-1.14***	-0.82***	No data	No data	0.62*	-0.47	-0.25	-0.25	No data	-0.39	-1.47***	-0.94***	
Diet breadth	No data	0.32	0.56***	0.35**	No data	No data	1.20*	0.93**	1.22**	1.22**	No data	0.84*	1.29***	1.13***	
(D) Body size															
Body mass ^L	0.31***	0.46***	0.47***	0.22***	-0.28	-0.01	-0.13	0.01	0.01	0.01	-0.00***	0.44***	0.24**	0.22***	
Body length ^L	1.01***	0.99***	0.41***	0.69***	-0.53	-1.39*	0.14	-0.25	-0.25	-0.25	0.47***	0.09***	0.54*	0.40***	
Relative brain mass	No data	-0.21	-0.47**	-0.42**	No data	No data	0.12	-0.33	-0.13	-0.13	No data	-0.16	-0.69	-0.46*	
(E) Life history															
Fecundity	0.19***	-0.13	1.35***	1.01***	-0.48***	0.98*	0.01 ^L	-0.25 ^{L†}	-0.25 ^{L†}	-0.25 ^{L†}	-0.12	0.27	1.20***	0.62 ^{L‡}	
Egg diameter, birth or egg mass ^L	1.21***	0.50**	0.35**	0.17 ^S	0.65	0.16	0.16	0.32 ^S	0.32 ^S	0.32 ^S	1.89***	0.63*	0.52	0.60 ^S	
Litter or clutch mass ^L	No data	0.58***	1.03***	0.32***	No data	No data	0.12	0.13	0.39	0.39	No data	0.68*	1.16	0.88***	
Litters or clutches per year	-0.16	0.42	0.35*	0.12	0.31	0.26	0.72	0.37	0.37	0.37	0.12	0.58	1.19	0.45	
Offspring per year ^L	0.09***	0.35	1.16***	N/A	-0.47**	0.55	0.28	N/A	N/A	N/A	-0.10	0.72	1.28**	N/A	
Parental care	0.56***	0.75 ^{L*}	-0.22 ^L	N/A	0.72*	0.06 ^L	-0.09 ^L	N/A	N/A	N/A	1.01***	0.77 ^{L*}	-0.23 ^L	N/A	
Age of first reproduction	0.33*	0.02	-0.18	0.11	-0.58	-0.40	0.05	-0.26	-0.26	-0.26	-0.22	-0.16	-0.12	-0.14	
Maximum lifespan ^L	0.84***	1.01***	0.43***	0.68***	-0.43	0.19	0.67	-0.01	-0.01	-0.01	0.19	1.09**	0.97**	0.61	
Sexual dimorphism	-0.27	0.93*	0.51***	0.38***	0.29	-1.13*	-0.08	-0.31	-0.31	-0.31	0.00	0.04	0.39	0.14	

Given are effect sizes *d* Gurevitch & Hedges (2001), e.g. the effect size for body mass in the column 'Which species are introduced?' for fish was calculated as: (mean body mass of introduced fish - mean body mass of nonintroduced fish) / pooled standard deviation of body mass of introduced and nonintroduced fish, where $J = 1 - 3 / (4 \cdot (N_{\text{all fish}} - 2) - 1)$, a correction factor for the smaller sample sizes in the column 'Of the introduced species, which are invasive?'. Positive values of *d* indicate higher values for the species that have taken the step of the invasion process compared to those that have not taken it, e.g. body mass was higher for introduced than for nonintroduced fish. Significant strong effects ($|d| \geq 0.8$, Gurevitch & Hedges (2001)) are highlighted by a grey background.

Independent of effect sizes, we also performed significance tests: two-tailed binomial tests in case of dichotomous variables (sexual dimorphism, carnivory, human affiliation, hunting), *U*-tests in case of the ordinate variable parental care in fish, and *t*-tests in case of metric variables (for unequal variances and/or with log₁₀-transformed data, if necessary: if a superscript L is given in the leftmost column of a row, all data were log₁₀-transformed for that row; if the superscript L is given in a single cell, only the data for that cell were log₁₀ transformed); **P* ≤ 0.05; ***P* ≤ 0.01; ****P* ≤ 0.001.

[†]The variable 'native continent Europe' is dichotomous where 1 indicates Europe and 0 indicates North America. Thus, a positive effect size in this case means that European species were more likely to take a step of the invasion process than North American species.

[‡]Fish are excluded here because their much higher fecundity is not comparable to mammals and birds.

[§]Offspring mass, which was estimated for fish from egg diameter by assuming spherical eggs and egg densities of 1 g cm⁻³.

more often introduced between the two continents than other species, which partly explains their higher invasion success. However, human affiliation was included together with propagule pressure in many of the final multivariate regression models, so it is still important when propagule pressure is factored out.

Game species had a significantly higher probability of being introduced to an exotic continent, while they tended to have a lower probability of spreading there. Thus, hunting influenced the different steps of the invasion process antagonistically. The total effect of hunting on invasion success was positive, although weaker than those of propagule pressure and human affiliation. The effect of hunting nearly disappeared in the phylogenetic analyses because humans tend to hunt phylogenetically related species (e.g. species of trout, hare, or waterfowl). The proportion of game species was 22.7% in fish, 18.0% in mammals, 21.7% in birds, and 21.3% in all species.

Population size and extent

Of the three variables in this group (population density, native latitudinal range, and native continent), latitudinal range had a relatively strong effect on invasion success, but only in the univariate analyses where it was strongly and positively correlated to introduction success, especially in fish and mammals. Its effect on steps 2 and 3 of the invasion process (establishment and spread) was small, but overall, it was strongly and positively correlated to invasion success in the univariate analyses. In the multivariate regressions, however, its overall effect on invasion success disappeared because latitudinal range is also significantly correlated to propagule pressure (fish: $r = 0.24$; mammals: $r = 0.28$; birds: $r = 0.19$; all species: $r = 0.25$; all $P < 0.001$, one-tailed), and propagule pressure was a stronger determinant of invasion success than latitudinal range. Thus, the extent of the native range of a species influences its likelihood to be introduced to an exotic continent and, as a result, its likelihood to become invasive.

The native continent (i.e. the direction of introduction) was not a strong determinant of invasion success. In the univariate analyses, this variable was consistently positively correlated to invasion success but effect sizes were small. In the multivariate analyses, the native continent was included in some of the final regression models but never as a strong predictor. It is nonetheless noteworthy that the direction of the effect differed between univariate and multivariate analyses: in the univariate analyses, European species tend to have a higher invasion success than North American species, but the opposite was true in the multivariate analyses. This apparent contradiction can be explained by the

significant correlation of the variable 'native continent' with human affiliation among the introduced species for most taxa (fish: $r_{sp} = 0.35$, $P < 0.05$; mammals: $r_{sp} = -0.14$, $P = 0.549$; birds: $r_{sp} = 0.34$, $P < 0.01$; all species: $r_{sp} = 0.27$, $P = 0.001$; all P two-tailed). In other words, a higher proportion of European than North American introduced species are human affiliates, which have a higher invasion success than species not affiliated with humans, as shown above. The positive correlation of the native continent of Europe with invasion success was, thus, apparently based on the high number of European human affiliates. This effect was factored out in the multivariate regressions where the native continent of North America led to a slightly higher invasion success.

Diet

Carnivorous mammals and birds had a lower invasion success than herbivores mainly because they had a lower introduction success. In mammals, carnivory even had antagonistic effects at the different steps: it disfavored introduction but favored establishment and spread.

Diet breadth was positively and significantly correlated to invasion success in the univariate analyses but disappeared as a predictor in the multivariate regressions probably because it was significantly correlated to human affiliation (mammals: $r_{sp} = 0.26$; birds: $r_{sp} = 0.15$; mammals and birds combined: $r_{sp} = 0.22$; all $P < 0.001$, two tailed).

Body size

None of the three variables included in this category (body mass, body length, and relative brain mass) was a good predictor of invasion success. Although they were significantly correlated to invasion success in the univariate analyses, their effect sizes were small (Table 1). Moreover, they were rarely included in the final multivariate regression models (Tables 2 and 3). Interestingly, however, body length antagonistically affected the invasion success of mammals at the different steps of the invasion process: it was positively correlated to introduction success but negatively correlated to establishment and spread success. These antagonistic effects balanced each other so that there was no meaningful influence of body length on overall mammal invasion success (Table 1).

Life history

What was observed for body length also applied to one of the nine life-history variables considered here, sexual

Table 2 Results of multivariate logistic regressions, uncorrected for phylogeny

	Which species are introduced?	Of the introduced species, which are invasive?	Of all species, which are invasive?
Fish ($N = 91$; Cox–Snell $R^2 = 0.37, 0.26$, respectively)	0.19 latitudinal range 0.94 egg diameter 2.84 human affiliation 0.99 parental care	Insufficient sample size ($N = 22$)	0.34 propagule pressure 0.90 egg diameter
Mammals ($N = 100$; Cox–Snell $R^2 = 0.25, 0.33$, respectively)	19.9 hunting 2.17 human affiliation –2.41 carnivory	Insufficient sample size ($N = 9$)	10.8 propagule pressure 118 human affiliation
Birds ($N = 327, 38, 327$, respectively; Cox–Snell $R^2 = 0.25, 0.24, 0.17$, respectively)	–1.74 carnivory 1.33 human affiliation 1.25 hunting 0.33 offspring per year 0.00 lifespan	0.25 propagule pressure	19.6 propagule pressure 0.60 clutch mass 139 clutches per year –0.25 body mass 1.95 egg mass
Mammals and birds ($N = 400, 47, 400$, respectively; Cox–Snell $R^2 = 0.23, 0.31, 0.17$, respectively)	1.72 hunting –1.95 carnivory 1.32 human affiliation 0.12 offspring per year 0.05 latitudinal range	3.56 human affiliation	0.55 propagule pressure 3.84 human affiliation 3.62 hunting –2.48 native continent Europe
All ($N = 1495, 100, 1495$, respectively; Cox–Snell $R^2 = 0.14, 0.15, 0.08$, respectively)	2.04 hunting 0.07 latitudinal range 1.52 human affiliation 1.11 sexual dimorphism	0.07 propagule pressure	0.17 propagule pressure 2.15 hunting 1.57 human affiliation 0.08 latitudinal range –1.30 native continent Europe

Notes: The regressions were run stepwise forward. Each cell gives the entry order of significant variables together with regression coefficients B .

dimorphism: it was positively correlated to introduction success of mammals but negatively to establishment and spread success, resulting in the absence of an effect on overall mammal invasion success (Table 1). In fish, maximum lifespan similarly was positively correlated to introduction success but negatively to spread success. In mammals and birds, maximum lifespan was positively correlated to introduction success, too, but also, at least slightly, to spread success so that it was overall positively correlated to invasion success. Other life-history variables that predicted invasion success for one of the taxa were egg diameter in fish and fecundity, clutch mass, and offspring per year in birds. However, most life-history variables were not good predictors of invasion success.

Discussion

Association with humans

We showed that the association with humans is generally a strong determinant of vertebrate invasion success. We subdivided this relationship into the three factors: propagule pressure, human affiliation, and hunting. Propagule pressure and human affiliation were the

two strongest determinants of invasion success. As outlined in the Introduction, the importance of propagule pressure is well known, and evidence for the influence of human affiliation on invasion success already exists as well. However, previous studies do not distinguish whether the success of human affiliates can be completely explained by or is partly independent of propagule pressure. Our results suggest the latter although it should be kept in mind that we rather crudely quantified propagule pressure as the number of countries, states, or provinces that a species was introduced to (see 'Materials and methods'). Also, insufficient data prevented us from analyzing all 20 variables that were included in the univariate analyses in the multivariate regressions. Human affiliation appears to be a stronger determinant of invasion success in mammals and birds than in fish, probably because aquatic organisms cannot directly benefit as much from the terrestrial species *Homo sapiens* as terrestrial mammals and birds. Our results nonetheless suggest that human affiliation is independently of propagule pressure a strong predictor of invasion success.

Human affiliation may even become more important in the future because the number of domesticates, pets, and human commensals appears to be rising. Generally

Table 3 Results of multivariate linear regressions of phylogenetically independent contrasts

	Which species are introduced?	Of the introduced species, which are invasive?	Of all species, which are invasive?
Fish ($N = 90$; Adjusted $R^2 = 0.38, 0.16$, respectively)	0.43 egg diameter 0.36 latitudinal range 0.22 human affiliation -0.18 native continent Europe	Insufficient sample size ($N = 21$)	0.41 propagule pressure
Mammals ($N = 99$; Adjusted $R^2 = 0.14, 0.51$, respectively)	-0.29 carnivory 0.21 maximum lifespan	Insufficient sample size ($N = 8$)	0.48 propagule pressure -0.33 carnivory 0.29 human affiliation -0.21 native continent Europe
Birds ($N = 326, 37, 326$, respectively; Adjusted $R^2 = 0.07, 0.55, 0.29$, respectively)	0.23 human affiliation 0.14 maximum lifespan	0.63 human affiliation 0.23 propagule pressure -0.54 body mass -0.42 offspring per year 0.27 latitudinal range	0.47 propagule pressure 0.17 human affiliation
Mammals and birds ($N = 399, 46, 399$, respectively; Adjusted $R^2 = 0.07, 0.52, 0.30$, respectively)	0.22 human affiliation 0.15 maximum lifespan	0.70 human affiliation -0.54 body mass -0.38 offspring per year 0.25 latitudinal range	0.44 propagule pressure 0.16 human affiliation -0.11 carnivory 0.09 latitudinal range -0.08 native continent Europe
All ($N = 1494, 99, 1494$, respectively; Adjusted $R^2 = 0.11, 0.29, 0.23$, respectively)	0.26 human affiliation 0.12 latitudinal range 0.08 body mass -0.05 native continent Europe	0.39 propagule pressure 0.20 sexual dimorphism 0.18 human affiliation	0.40 propagule pressure 0.14 human affiliation 0.08 latitudinal range 0.07 sexual dimorphism -0.07 native continent Europe 0.06 hunting

Notes: The regressions were run stepwise forward. Each cell gives the entry order of significant variables together with standardized regression coefficients β .

speaking, the list of human affiliates is dynamic. The degree to which a species is affiliated with humans can change over time as a result of changes in the species or changes in human preferences. Many species that were not formerly affiliated with humans have now adapted to humans in various ways and are strongly associated with them; beech martens, herring gulls, and Canada geese are familiar examples. The number of such commensals will probably keep rising through time as more and more wild species adapt to take advantage of an increasingly human-dominated landscape. Human preferences for pets and domestic animals change over time as well, and many species formerly exclusively seen in zoological gardens are now routinely kept as pets or domestic animals (e.g. ferrets or llamas). Again, it seems likely that the diversity of pets and domestic animals is rising through time.

Imperialism dogma and resistance hypothesis

In contrast to the association with humans, the native continent of a species apparently is not a strong deter-

minant of vertebrate invasion success, and neither is the continent where a species is introduced (cf. Jeschke & Strayer, 2005). These negative results may be surprising because they question the applicability of two major hypotheses in invasion biology, the imperialism dogma and the resistance hypothesis. The imperialism dogma states that Eurasian species have a higher invasion success than species from other continents because they coevolved with Europeans and their plants, pathogens, and livestock, which were dispersed all over the world during the European imperialism period from 900 to 1900. Thus, if a Eurasian species is introduced to a new range, it is likely confronted with species it has coevolved with (Crosby, 1986; Simberloff, 2004; Jeschke & Strayer, 2005). This hypothesis is partly supported by our results because we showed that European species tend to be slightly more invasive than North American species due to their higher degree of human affiliation which, in turn, is probably based on coevolution with Europeans. On the other hand, the overall effect on invasion success was weak, which questions the practical importance of the imperialism effect in vertebrates.

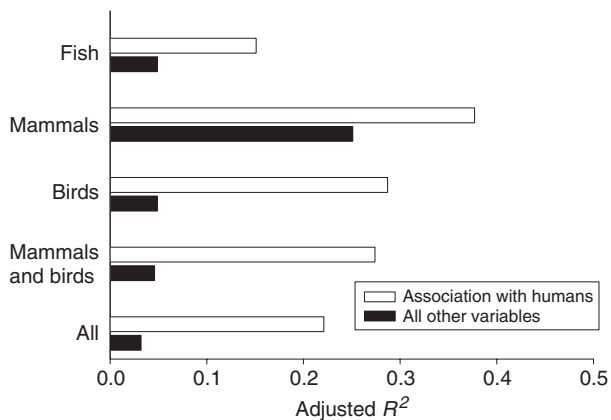


Fig. 1 Adjusted R^2 -values of regressions of phylogenetically independent contrasts looking at which species of all are invasive. The regressions shown were done in the same way as those underlying the right column in Table 3 except that different independent variables were chosen and these were all part of regression models (no stepwise entry or removal of variables; sample sizes as given in Table 3). The variables directly associated with humans were propagule pressure, human affiliation, and hunting.

The second major hypothesis of invasion biology that is relevant here is the resistance hypothesis which states that less disturbed and richer biota offer more resistance to invaders (Elton, 1958; Starfinger, 1998; Levine & D'Antonio, 1999; Mack *et al.*, 2000; Cox, 2004; Zavaleta & Hulvey, 2004; Jeschke & Strayer, 2005; Stachowicz & Tilman, 2005). Applied to our study, this would mean that North America is more resistant to invaders than Europe, so European species introduced to North America should have a lower invasion success than North American species introduced to Europe. Indeed, the multivariate analyses shown here support this hypothesis. But again, the quantitative effect on invasion success was weak.

Sexual dimorphism

Analyzing the importance of sexual dimorphism to invasion success allows evolutionary insights, for sexual dimorphism can be used as a conservative indicator for the intensity of sexual selection (Andersson, 1994; McLain *et al.*, 1995, 1999; Sorci *et al.*, 1998; Cassey, 2002; Cassey *et al.*, 2004c; Fisher & Owens, 2004). Sexual selection is usually assumed to work in opposition to natural selection: 'Conspicuous secondary sex traits may often be favored only or mainly by sexual selection and counteracted by other natural selection.' (Andersson, 1994, p. 8) One could, therefore, expect a higher invasion success of species with weak sexual selection which are not sexually dimorphic. In line with this expectation are the studies by McLain *et al.* (1995,

1999), Sorci *et al.* (1998), and Cassey (2002) who observed significant negative correlations between establishment success and sexual dichromatism in birds. On the other hand, Cassey *et al.* (2004c) and Donze *et al.* (2004) found no such significant correlation, and neither did we in the current study: sexual dimorphism in birds was not significantly correlated to establishment and spread success. On the other hand, it was significantly positively correlated to introduction success in the univariate analyses (Table 1), probably reflecting human preference for showy birds. To our knowledge, no previous study looked at the relationship between invasion success and sexual dimorphism in other taxa than birds. In mammals, we found as in birds a significant positive correlation to introduction success in the univariate analyses which may again be explained by human preference. In contrast to birds, however, we found a significant negative correlation to establishment and spread success. These antagonistic effects at the different steps of the invasion process balanced each other so that the overall effect on invasion success was negligible (Table 1). Finally, there was no apparent effect on any step of the invasion process in fish. In interpreting these results, one should consider that we classified species as being dimorphic or monomorphic according to our human visual sense, which is the relevant sense for the selection of species for introduction. The visual sense of the analyzed species differs from the human one, however, so species that appear monomorphic for humans may be dimorphic for the individuals of that species (Eaton, 2005). This methodological difficulty is a reason why sexual dimorphism as classified here and in all other similar studies should be used only cautiously as an indicator for the intensity of sexual selection. Accordingly, we tentatively conclude that the results presented here do not consistently support the hypothesis that species with intense sexual selection are at a disadvantage against species with weak sexual selection.

The first step of invasion: introduction

Of the three steps of the invasion process (introduction, establishment, and spread), the first step is the least investigated but perhaps the most important one (Jeschke & Strayer, 2005; Puth & Post, 2005). Certainly, for some questions about deliberately introduced species, knowledge about this step is not particularly important. For example, if one has to decide whether a species proposed for introduction should be allowed to enter a country, one is mainly interested in the second and third steps of the invasion process. But because many species introductions are accidental (US Congress, 1993), the investigation of the first step has

numerous applied benefits. For instance, knowledge of species with a high potential to enter a country (and to subsequently spread) allows for an increased vigilance against such high-risk species not only at airports, harbors, and other entry points, but also within a country. As a result, fewer individuals of high-risk species will enter, and those that do enter will be detected earlier. This early detection is very important because eradication success drops quickly with time (Mack *et al.*, 2000; Simberloff *et al.*, 2005). Many basic questions on invasive species can only be addressed by looking at all steps of the invasion process (e.g. 'Why are some species invasive and others not?' and 'What makes a species invasive?') Especially because some factors have antagonistic effects at each step, it is necessary to investigate the complete invasion process, as did Cassey *et al.* (2004b) and our study. Critically, only these two studies investigated the correlates of species traits to invasion success for the complete invasion process.

Outlook

We call for more studies that look at all steps of the invasion process or at least the first step (introduction), which is underrepresented in the literature. Besides the consideration of the complete species pool available for introduction, another strength of the current study is the inclusion of thousands of species of three major taxa and of many traits for each of these species. For example, only by including both propagule pressure and human affiliation was it possible to detect that human affiliation is a strong predictor of invasion success independently of propagule pressure. Future studies should test this finding but preferably with a more exact quantification of propagule pressure as was possible here. Comprehensive analyses of the determinants of invasion success should also include factors that have usually been left aside (e.g. parasitic load (Mitchell & Power, 2003; Torchin *et al.*, 2003), immune responses (Lee & Klasing, 2004), or the fauna of the receiving community (Cassey *et al.*, 2005)). Such approaches may lead to stronger predictive models of invasion success.

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