Invasion success of vertebrates in Europe and North America

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Species become invasive if they (*i*) are introduced to a new range, (*ii*) establish themselves, and (*iii*) spread. To address the global problems caused by invasive species, several studies investigated steps *ii* and *iii* of this invasion process. However, only one previous study looked at step *i* and examined the proportion of species that have been introduced beyond their native range. We extend this research by investigating all three steps for all freshwater fish, mammals, and birds native to Europe or North America. A higher proportion of European species entered North America than vice versa. However, the introduction rate from Europe to North America peaked in the late 19th century, whereas it is still rising in the other direction. There is no clear difference in invasion success between the two directions, so neither the imperialism dogma (that Eurasian species are exceptionally successful invaders) is supported, nor is the contradictory hypothesis that North America offers more biotic resistance to invaders than Europe because of its less disturbed and richer biota. Our results do not support the tens rule either: that ≈10% of all introduced species establish themselves and that ≈10% of established species spread. We find a success of ≈50% at each step. In comparison, only ≈5% of native vertebrates were introduced in either direction. These figures show that, once a vertebrate is introduced, it has a high potential to become invasive. Thus, it is crucial to minimize the number of species introductions to effectively control invasive vertebrates.

biotic resistance | ecological imperialism | invasive species | tens rule | time lags

Humans transport organisms all over the world and thereby introduce species to ranges they would not otherwise occupy. Some of these introductions are beneficial, e.g., corn, but many others have been condemned, such as rats and other invasive species (1–10). To become invasive, a species must take three steps: (*i*) introduction, (*ii*) establishment, and (*iii*) spread (11). Although steps *ii* and *iii* have been well investigated (4, 11), only Cassey *et al*. (12, 13) looked at step *i* and examined the proportion of species that have been introduced beyond their native range. We extend this research by examining all three steps for all freshwater fish, mammals, and birds that are native to either Europe or North America. Because these regions are particularly well investigated and vertebrates are particularly noticeable organisms, good records are available, even for failed introductions. We address the following specific questions. (*i*) When were fish, mammals, or birds native to Europe or North America introduced to the other continent? (*ii*) How many species were introduced in either direction? (*iii*) How many of the introduced species established themselves in the nonnative continent, and how many established species spread? (*iv*) Is invasion success asymmetric between the continents?

Our specific hypotheses are as follows. (*i*) Introductions to North America started earlier than those to Europe. This hypothesis is based on historical patterns of human immigration. (*ii*) Less than 15% of the vertebrate species were introduced between Europe and North America. Cassey *et al*. (12) found that, of all 350 extant species of parrots, 54 (15%) were introduced into an alien environment. Because parrots are popular pets and can easily escape their owners, we suggest that 15% is a reasonable upper limit on vertebrate introductions. We know of no other study that gives proportions of species introductions. (*iii*) The tens rule of Williamson (4) says that ≈10% of the introduced species establish themselves in the nonnative continent and that ≈10% of these, in turn, spread or are pests. Strictly speaking, the tens rule says that ≈10% (5–20%) of the established species become pests rather than spread. However, Williamson offers no definition for pest and writes that there is much disagreement on this term. He distinguishes between pests in general and severe pests, so his term pests is not restricted to severe pests. For simplicity, we here use pests as synonymous to invasive species, which we define as those species that spread beyond their native range. In contrast to some other definitions (14), invasive species as defined here are not necessarily harmful. Readers who think that the group of invasive species is larger than the group of pests may adjust the 10% (5–20%) estimation upward, maybe to 10–20%. (*iv*) "Eurasian species are at an advantage everywhere" (15). This now "common dogma" (15) was introduced by Crosby in his book *Ecological Imperialism* (16). We therefore call it the imperialism dogma. It is based on two observations: first, Eurasian species coevolved with Europeans and their plants, pathogens, and livestock, which were, second, 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. On the other hand, the biota of North America is less disturbed by humans and richer than that of Europe and could thus offer more resistance to invaders (1, 6, 17–19). We call this alternative to the imperialism dogma the resistance hypothesis.

Materials and Methods

To test these hypotheses, we created a list of all freshwater fish, mammals, and birds that are native to Europe or North America, where native is defined as being established before the year 500. Although we used the ordinary geographical definition for Europe, we defined North America as Canada plus the United States except Hawaii. Migrating birds were included if they breed in Europe or North America. Fish species were included if they spend all or much of their lives in fresh water. This category includes diadromous species but not casual visitors to fresh waters. We then excluded those species that are native to both continents and gathered information on when and how many of the remaining ≈2,400 species were introduced between the two continents and how many of these introduced species established themselves and spread. Dates of introduction relate to the first release into the wild; introductions in the 21st century are not included. The resulting species list (with references) is available in Data Set 1, which is published as supporting information on the PNAS web site.

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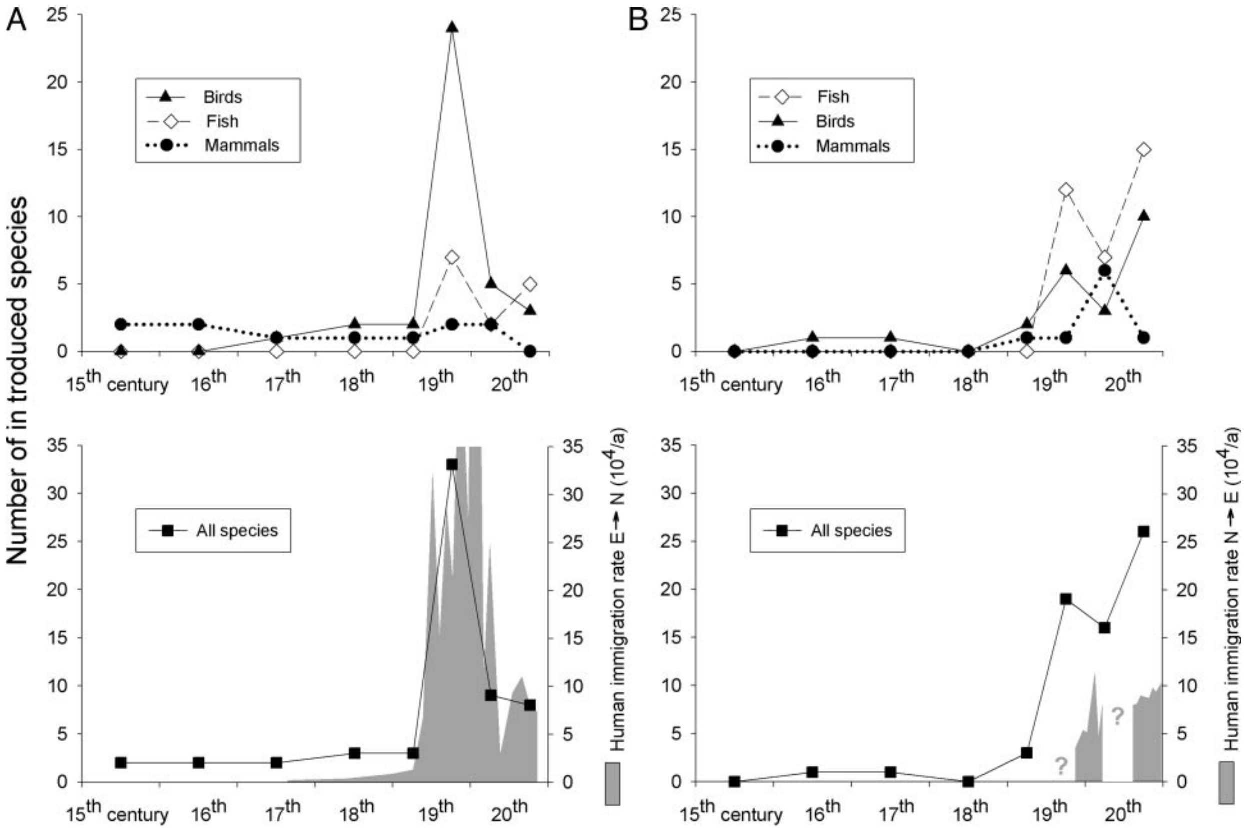

Fig. 1. Temporal patterns of vertebrate introductions from Europe to North America (*A*) and vice versa (*B*). Up to the 18th century, the numbers of introductions are given per century because of the rarity of these events. For the 19th and 20th centuries, the numbers of introductions are given per half century. Human immigration rate data are from refs. 20–26; missing data are indicated by question marks.

Although Europe and North America are particularly well investigated and vertebrates are particularly noticeable, unrecorded introductions do nonetheless exist and could influence our analysis. To estimate their number for each continent and taxon, we counted the number of established species for which no independent introduction record is available, i.e., whose introduction would have remained unknown if the species had not established. For example, for 2 of the 19 established North American fish species in Europe, no independent introduction record is available. The 17 remaining established species arose from recorded introductions of 35 species. If we assume that establishment success is independent of whether an introduction was recorded, we can estimate the total number of introductions x as $x = [(\text{number of established species})/(\text{number of recorded introduced species that established})] \times (\text{total number of recorded introduced species})$; e.g., $x = (19/17) \times 35 \approx 39$. To test the influence of unrecorded introductions on our results, we repeated our analysis with the estimated total number of introductions.

Another complication that might influence our results is that recently introduced species may not have established themselves or spread because they have not had enough time to do so. By excluding such recent introductions, we corrected for time-lags. What recent means, however, differs between the vertebrate groups because they differ in the length of their time-lags. For each group, we estimated the time-lag by comparing the mean year of introduction of all introduced species (mean step *i* year) with that of all established species (mean step *ii* year) and that

Table 1. Vertebrate introductions between Europe and North America

Invasion step	No. of species Europe → North America: Fish (n = 220)	Mammals (n = 207)	Birds (n = 361)	All (n = 788)	No. of species North America → Europe: Fish (n = 713)	Mammals (n = 342)	Birds (n = 519)	All (n = 1,574)	World parrots (ref. 12) (n = 350)
Introduction	14	13	40	67	35	9	28	72	54
	6.4 ± 3.2%	6.3 ± 3.3%	11.1 ± 3.2%	7.9 ± 1.9%	4.9 ± 1.7%	2.6 ± 1.7%	5.4 ± 1.9%	4.3 ± 1.0%	15.4 ± 3.8%
Establishment	9	11	12	32	19	7	7	33	38
	64.3 ± 25.1%	84.6 ± 19.6%	30.0 ± 14.2%	59.6 ± 11.6%	54.3 ± 16.5%	77.8 ± 27.2%	25.0 ± 16.0%	52.4 ± 11.9%	70.4 ± 12.2%
Spread	5	8	8	21	12	5	2	19	N/A
	55.6 ± 32.5%	72.7 ± 26.3%	66.7 ± 26.7%	65.0 ± 16.5%	63.2 ± 21.7%	71.4 ± 33.5%	28.6 ± 33.5%	54.4 ± 17.4%	N/A

The given percentages [±95% confidence interval (C.I.), binomial distribution] are based on the species that made the previous step of the invasion process. For example, from the pool of 220 fish species native to Europe but not to North America, 14 were introduced to North America, i.e. 6.4%. The calculations for All species are based on the proportions for fish, mammals, and birds. For example, the given proportion of all species that were introduced from Europe to North America was calculated as the mean for fish (6.4%), mammals (6.3%), and birds (11.1%) rather than as the ratio of 67 to 788; here, the 95% C.I. was calculated by assuming independence of fish, mammal, and bird introductions. The study by Cassey *et al.* (12) on worldwide parrot introductions is given for comparison.

Table 2. As Table 1, but corrected for unrecorded introductions (see *Materials and Methods*)

	No. of Species Europe → North America				No. of species North America → Europe			
Invasion step	Fish (n = 220)	Mammals (n = 207)	Birds (n = 361)	All (n = 788)	Fish (n = 713)	Mammals (n = 342)	Birds (n = 519)	All (n = 1,574)
Introduction	25	13	40	78	39	9	39	87
	11.4 ± 4.2%	6.3 ± 3.3%	11.1 ± 3.2%	9.6 ± 2.1%	5.5 ± 1.7%	2.6 ± 1.7%	7.5 ± 2.3%	5.2 ± 1.1%
Establishment	9	11	12	32	19	7	7	33
	36.0 ± 18.8%	84.6 ± 19.6%	30.0 ± 14.2%	50.2 ± 10.2%	48.7 ± 15.7%	77.8 ± 27.2%	17.9 ± 12.0%	48.1 ± 11.2%
Spread	5	8	8	21	12	5	2	19
	55.6 ± 32.5%	72.7 ± 26.3%	66.7 ± 26.7%	65.0 ± 16.5%	63.2 ± 21.7%	71.4 ± 33.5%	28.6 ± 33.5%	54.4 ± 17.4%

n, no. of species in the native pool.

of all invasive species (mean step *iii* year): for fish, the difference between the mean step *i* year and the mean step *ii* year is 13 years, whereas the difference between the mean step *i* year and the mean step *iii* year is 12 years. The corresponding numbers for mammals are 14 and 62 years; those for birds are 52 and 60 years. That is, fish and mammals need slightly longer than a decade to establish themselves, whereas birds need five decades. The difference between establishment and spread seems negligible for fish and also small for birds, but is five decades for mammals. To test the influence of time-lags on our results, we repeated our analysis by restricting it to introductions before 1990 for fish and before 1940 for mammals and birds.

To assess the generality of our results, we compare them with previous studies on the proportions of introduced animals that established themselves and of established animals that spread. For this comparison, we selected studies representing a broad range of taxonomy, geography, and introduction mode.

Results and Discussion

Time Patterns. Vertebrate introductions between Europe and North America were temporally variable and asymmetric (Fig. 1). Introductions from Europe to North America were dominated by mammals in the 15th and 16th century, birds in the 18th, 19th, and early 20th century, and fish in the late 20th century (Fig. 1*A*). Introductions from North America to Europe were dominated by birds until the early 19th century and by fish thereafter (Fig. 1*B*). The total introduction rate to North America outnumbered that to Europe through the 19th century, but the reverse was true for the 20th century. Similarly, the qualitative temporal dynamics in each direction were similar through the 19th century but diverged in the 20th century.

These patterns are consistent with hypothesis *i* and with previous analyses. According to Kegel (8), mammal and bird introductions peaked in the 19th century when acclimatization societies introduced basically every species they liked from home, i.e., Europe, to wherever they were living at that time. In contrast, worldwide fish introductions peaked in the 1960s (3). This observation is broadly consistent with our results, although the highest number of fish introductions from Europe to North America occurred in the late 19th century.

Why did the introduction rate to North America outnumber that to Europe through the 19th century but not thereafter? From the 15th to the early 20th century, European imperial states dominated the world (27). As a result, Europeans and their organisms arrived nearly everywhere (16). Europeans were also the major immigrants to North America in this time period. The number of immigrants fits well to the number of species introduced (Fig. 1*A*): about one European vertebrate species was introduced to North America per 10,000 human immigrants. After World War I, North America became more and more powerful (27). The number of European immigrants decreased, and so did the number of species introductions. By contrast, the number of North American immigrants to Europe has been increasing through time, so there is a qualitative match to the increase in species introductions (Fig. 1*B*). Quantitatively, about one North American vertebrate species was introduced to Europe per 4,000 human immigrants. In other words, after controlling for the number of human immigrants, there have been more species introductions from North America to Europe than vice versa. This difference may be based on different laws and attitudes concerning introduced species, including the imperialism dogma (which implies that non-Eurasian species are not particularly dangerous when introduced). An alternative explanation is that some species were not introduced by human immigrants but by the people of the target continent, e.g., turkeys (*Meleagris gallopavo*) introduced to Europe (2). More species were probably introduced in this way to Europe than to North America, which may at least partly explain the introduction bias toward Europe when human immigration is controlled for.

Invasion Success. The absolute total number of fish, mammals, and birds introduced between Europe and North America is about the same in each direction, roughly 70 (Table 1). About twice as many vertebrate species are native to North America as to Europe. When the number of introductions is scaled to the

Table 3. As Table 1, but corrected for time-lags by restricting it to introductions before 1990 for fish and before 1940 for mammals and birds (see *Materials and Methods*)

	No. of species Europe → North America				No. of species North America → Europe			
Invasion step	Fish (n = 220)	Mammals (n = 207)	Birds (n = 361)	All (n = 788)	Fish (n = 713)	Mammals (n = 342)	Birds (n = 519)	All (n = 1,574)
Introduction	12	13*	37*	64*	34	7	14*	58*
	5.5 ± 3.0%	6.3 ± 3.3%	10.2 ± 3.1%	7.3 ± 1.8%	4.8 ± 1.6%	2.0 ± 1.5%	2.7 ± 1.4%	3.2 ± 0.9%
Establishment	7	11	10	30	19	5	4*	30*
	58.3 ± 27.9%	84.6 ± 19.6%	27.0 ± 14.3%	56.7 ± 12.3%	55.9 ± 16.7%	71.4 ± 33.5%	28.6 ± 23.7%	52.0 ± 14.8%
Spread	3	8	6	19	12	3	1	18
	42.9 ± 36.7%	72.7 ± 26.3%	60.0 ± 30.4%	58.5 ± 18.1%	63.2 ± 21.7%	60.0 ± 42.9%	25.0 ± 42.4%	49.4 ± 21.4%

n, no. of species in the native pool.
*Includes species for which no date of introduction was available. All such cases were treated as introductions before 1940.

native species pool, we get an introduction frequency of 7.9% for European species and 4.3% for North American species, a significant bias toward introductions from Europe to North America ($P < 0.01$, one-tailed exact test) and support of our hypothesis *ii* that all vertebrate species have been less frequently introduced than parrots. These results hold true if we consider unrecorded introductions (Table 2).

The proportions of species that take each step of the invasion process differ strongly: step *i*, introduction, clearly has been the hardest to take. For either direction of introduction, the proportion of all species that took step *i* is significantly lower than those that took step *ii* or *iii* (all $P < 0.001$, two-tailed exact tests). The same is true if we consider unrecorded introductions or time-lags between the dates of introduction, establishment, and spread (Tables 2 and 3).

Our results question the tens rule (4), which served as hypothesis *iii* for the success of alien animals at steps *ii* (establishment) and *iii* (spread). Mean establishment success far exceeds 10%: 59.6 ± 11.6% for introductions from Europe to North America and 52.4 ± 11.9% for the opposite direction (Table 1). Mean spread success similarly exceeds 10%: the numbers here are 65.0 ± 16.5% and 54.4 ± 17.4%, respectively. Our results are consistent with other animal data, implying that the tens rule does not hold for animals in general (Fig. 2). Certainly, some of the estimates of establishment success in Fig. 2 must be too high due to unrecorded species introductions. If the actual number of introduced species is higher than reported, actual establishment success is lower than reported. However, if we estimate the number of unrecorded introductions for the species analyzed here and reduce establishment successes accordingly, the numbers still far exceed 10% (Table 2). Furthermore, the data for spread success given in Fig. 2 are not affected by unrecorded species introductions and also violate the tens rule. This rule seems to hold for plants (4, 32), however, suggesting that introduced animals are more likely to establish themselves in a new environment than plants and are more likely to spread after establishment. This difference merits further attention. Presently, we can only speculate that it may arise from food web interactions or human introduction bias, i.e., differences in the nature of the pools of plant and animal species that humans transport and differences in the geographic locations or ecological communities into which plants and animals are introduced (14).

Fewer North American birds spread in Europe than European birds in North America (Table 1). This is the case for previous introductions, but the small sample size does not allow meaningful significance tests, so we cannot say with confidence whether this observation will hold for future bird introductions. Whereas past bird introductions support the imperialism dogma, Table 1 shows no clear differences between Europe and North America in the success of steps *ii* and *iii* for fish or mammals. If we consider time-lags, mammal introductions are consistent with the imperialism dogma, but fish introductions with the contradictory resistance hypothesis (Table 3). Fish also agree with the resistance hypothesis if Table 1 is modified to account for unrecorded introductions (Table 2). Thus, neither the imperialism dogma nor the contradictory resistance hypothesis is consistently supported by our results. It is possible, however, that these hypotheses apply to selected subsets of species or that the effects are weak or balance one other. Our analysis does not address the question of whether the impacts of invaders are influenced by ecological imperialism or biotic resistance.

In conclusion, our results question the tens rule, the imperialism dogma, and the resistance hypothesis. They show the critical importance of step *i* of the invasion process: introduction. Vertebrates have by far the lowest success in taking this step, so the most effective control of their invasion is to prevent them from entering a new range. Once they are introduced, vertebrates have a high potential to establish themselves and spread. We thus urge scientists and policy makers to create more effective barriers against inadvertent species introductions.

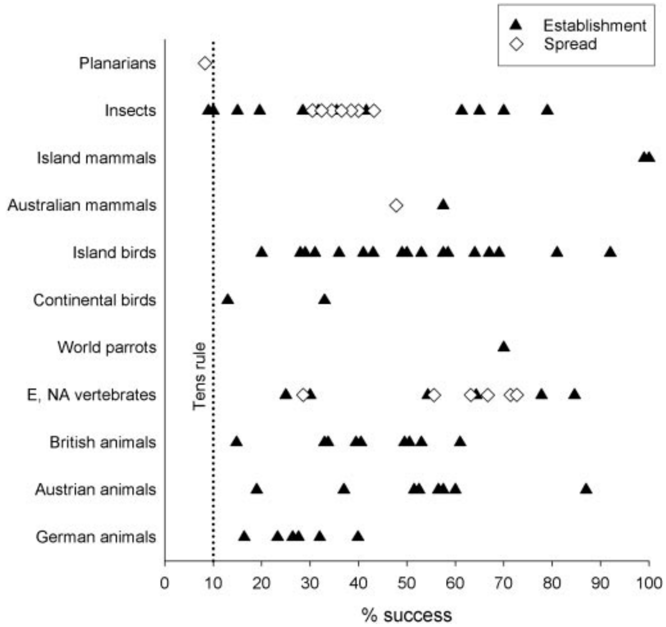

Fig. 2. Proportions of introduced animals that establish themselves (establishment success) and of established animals that spread or are pests (spread success). The tens rule predicts a 10% success for either step (vertical dotted line). Planarians, alien terrestrial planarians established in the U.K. (28); insects, biocontrol insects, symbols denote different diets and propagule pressures (4); island mammals, mammals introduced to Ireland and Newfoundland (4); Australian mammals (29); island birds, symbols denote different islands (30); continental birds, birds introduced to continental USA and Australia; world parrots, worldwide parrot introductions (12); E, NA vertebrates, European/North American vertebrates according to Table 1 (this study); British animals, symbols denote different taxa (31); Austrian animals, symbols denote different taxa (9); German animals, symbols denote different native continents (10).

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