

# Introduction pathways and establishment rates of invasive aquatic species in Europe

E. García-Berthou, C. Alcaraz, Q. Pou-Rovira, L. Zamora, G. Coenders, and C. Feo

**Abstract:** Species invasion is one of the leading mechanisms of global environmental change, particularly in freshwater ecosystems. We used the Food and Agriculture Organization's Database of Invasive Aquatic Species to study invasion rates and to analyze invasion pathways within Europe. Of the 123 aquatic species introduced into six contrasting European countries, the average percentage established is 63%, well above the 5%–20% suggested by Williamson's "tens" rule. The introduction and establishment transitions are independent of each other, and species that became widely established did so because their introduction was attempted in many countries, not because of a better establishment capability. The most frequently introduced aquatic species in Europe are freshwater fishes. We describe clear introduction pathways of aquatic species into Europe and three types of country are observed: "recipient and donor" (large, midlatitude European countries, such as France, the United Kingdom, and Germany, that give and receive the most introductions), "recipient" (most countries, but particularly southern countries, which give few species but receive many), and "neither recipient nor donor" (only two countries). A path analysis showed that the numbers of species given and received are mediated by the size (area) of the country and population density, but not gross domestic product per capita.

**Résumé :** L'invasion des espèces exotiques constitue l'un des mécanismes principaux de modification des environnements à l'échelle globale, particulièrement dans les écosystèmes d'eau douce. Nous avons utilisé la banque de données DIAS (Database of Invasive Aquatic Species) sur les espèces aquatiques envahissantes de l'Organisation des Nations unies pour l'alimentation et l'agriculture (FAO) pour déterminer les taux de transition des invasions et analyser les voies d'invasion en Europe. Le pourcentage d'établissement des 123 espèces aquatiques introduites dans six pays européens à caractère très différent est en moyenne de 63 %, bien au-delà des 5–20 % suggérés par la règle des dix pour cent de Williamson. Les transitions de l'introduction et de l'établissement sont indépendantes l'une de l'autre et les espèces qui deviennent établies sur une grande échelle le font parce que leur introduction a été tentée dans plusieurs pays et non parce qu'elles ont une meilleure capacité d'établissement. Les espèces aquatiques qui sont le plus souvent introduites en Europe sont les poissons d'eau douce. Nous décrivons des voies précises d'introduction des espèces aquatiques en Europe et nous plaçons les pays en trois typologies, les pays « receveurs et fournisseurs » (des pays européens des latitudes moyennes à grande superficie, tels que la France, le Royaume-Uni et l'Allemagne, qui fournissent et reçoivent la majorité des invasions), les « receveurs » (la plupart des pays, particulièrement ceux du sud, qui fournissent peu d'espèces, mais qui en reçoivent beaucoup) et les pays « qui ne reçoivent ni ne fournissent » d'espèces envahissantes (deux pays seulement). Une analyse des coefficients de direction montre que les nombres d'espèces fournies et reçues sont fonction de la superficie et de la densité de population du pays, mais non du produit national brut par habitant.

[Traduit par la Rédaction]

## Introduction

After loss of habitat, invasive species are the second leading cause of biodiversity loss, particularly in freshwater ecosystems (Moyle et al. 1986; Vitousek et al. 1997; Mack et al.

2000). Besides imposing huge economic costs, invasive species cause extinction of native species, reduction of genetic diversity, and biotic homogenization through a variety of mechanisms (Rahel 2000). There are three main stages in the invasion process: the intentional or unintentional introduction to the wild of a species imported into a region beyond its native range; the establishment of self-sustaining, reproductive populations; and population growth and spreading of the species (hereinafter introduction, establishment, and invasion transitions, respectively) (Richardson et al. 2000; Kolar and Lodge 2001). When defining the invasive transition it is better not to consider the ecological or socioeconomic impacts (Richardson et al. 2000; Rejmánek et al. 2002).

Williamson and coauthors (Williamson 1996; Williamson and Fitter 1996) proposed the "tens" rule for invasive species, which states that about 10% (between 5% and 20%) of the species succeed in each of the three transitions (i.e., from

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imported to introduced, from introduced to established, and from established to species with negative socioeconomic effects). Despite the vast literature and great ecological impact of freshwater invasions, the tens rule has been mostly evaluated for terrestrial plants, birds, and biocontrol insects (Williamson 1996; Kolar and Lodge 2001; Lockwood et al. 2001). Although the tens rule is a rule of thumb, there are previous formal tests of the rule (Lockwood et al. 2001), and the exceptions to the rule help to improve our understanding of invasion biology (Williamson 1996). Well-known deviations from the rule are intentionally introduced organisms such as edible crop plants and insects for biological control, which are intentionally introduced and selected by humans to be successful in the receiving ecosystem and, not surprisingly, a higher percentage established (Williamson 1996). Only about 13% of aquatic introductions in Europe are accidental (Welcomme 1992), but it has not been demonstrated whether they deviate from the rule, as would probably be expected.

The two most frequent approaches to the study of invasion biology are identifying species traits that might predict invasion success (Williamson and Fitter 1996; Mack et al. 2000; Kolar and Lodge 2001) and identifying attributes of communities that affect their susceptibility or resistance to invasion (Levine and D'Antonio 1999). In general, the results of these two approaches, mostly based on plants, have often been inconclusive (Williamson 1996, 1999; Smith et al. 1999), and the identification of predominant donor regions and invasion pathways has been recently suggested as a key element to increase the predictive ability of invasion biology (Jenkins 1996; Ricciardi and Rasmussen 1998; MacIsaac et al. 2001), particularly for aquatic invasions (Ricciardi and MacIsaac 2000). This new paradigm seems to be particularly important for taxa such as fishes, whose introductions are mostly not accidental but mediated by human interests. Deliberate introduction implies strong selection of particular taxa and donor and recipient regions, and establishment success should be expected to be higher and less dependent on the features of the species or the receiving ecosystem (Duncan et al. 2003).

Introduction effort, or propagule pressure, is a fundamental but elusive element of this new approach to invasion biology (Williamson 1996; Ricciardi and MacIsaac 2000; Ruiz and Carlton 2003). Unfortunately, in most introductions the number of individuals is often not known (Cassey et al. 2004), and introduction is the least studied of the three invasion transitions despite its alteration being probably the most practical way to mitigate the problem (Kolar and Lodge 2001). The number of species introductions attempted might be a proxy of propagule pressure when this is difficult to measure. Moreover, identification of key donor regions may help to prevent further introductions of new species and to control or eradicate new introductions in the initial phases, when it is more effective (Moody and Mack 1998). Because the geographical distribution of nonmigratory freshwater fish is enormously constrained by watersheds, fish can serve as indicators of introduction pathways for other invasive aquatic taxa that are less known or that expand their distribution range without human intervention.

The objectives of our paper are (i) to analyze invasion rates of aquatic species in Europe and compare establishment rates using Williamson's tens rule; and (ii) to identify

donor regions and invasion pathways within Europe and identify factors that determine which countries act as invasion sources or destinations.

## Methods

We used the United Nations Food and Agriculture Organization's Database of Invasive Aquatic Species (DIAS) as the main source of data. DIAS originally considered only freshwater fish species and the records have been published in full by Welcomme (1988) and described without statistical analyses in Welcomme (1991, 1992). The database was later expanded to include other freshwater and marine taxa and nowadays contains about 3200 records (81.9% fishes, 9.4% molluscs, 6.0% crustaceans, and the rest other taxa) that can be searched through the Internet (<http://www.fao.org/waicent/faoinfo/fishery/statist/fisoft/dias/mainpage.htm>). Of 566 introductions of 113 species in DIAS, 72.5% were intentional, 13% were accidental, and 14.5% occurred for unknown reasons (Welcomme 1991); an updated search of DIAS yielded 3200 introductions, of which 9% were accidental and 17% occurred for unknown reasons. For each species introduction, the database includes, when known, the countries of origin and destination, the year of introduction, whether the species established in the wild, and whether it had ecological effects in the recipient country. From the DIAS database, we made the following changes: "established in the wild through continuous restocking" to "not (naturally) established in the wild"; "probably established" to "established" or similar statements ("unknown" was not changed); we replaced time intervals during the year of introduction with the midpoint; and we did not consider the subspecific level. DIAS records "beneficial" and "adverse" ecological effects, but these qualifications would be controversial and we simply regarded both as ecological effects.

In the DIAS database, three stages were available: introduction, establishment, and occurrence of ecological effects. DIAS clearly underestimates the total number of species introductions, particularly of plants and invertebrates and those not established (e.g., some individuals of many tropical aquarium fish species are probably released unsuccessfully to the wild each year without record); it also probably underestimates the occurrence of ecological effects, which is based on subjective evidence. Of 3141 introduction records in the DIAS database, it is "unknown" whether the species succeeded in establishing in 13.9% of the records and whether it had ecological effects in 80%. The number of species imported into a country is also largely unknown and not reported in DIAS. Finally, Williamson (1996) described the tens rule for a "pest" transition (i.e., established introduced species causing negative socioeconomic effects) instead of the invasion transition. For all these reasons, this paper will focus on the establishment transition and will only briefly discuss the introduction transition and the existence of ecological effects. In the Discussion, we comment on the potential for bias in the overall percentages, which should be regarded with caution. Our approach is comparative, rather than to estimate absolute figures, because we consider that when comparing continents, countries, or the different roles played by a country's area, latitude, or population density, the general conclusions are unaffected by the biases.

**Table 1.** Invasion transitions of the 10 most frequently introduced aquatic species in the world plus 2 additional species (obtained from the Food and Agriculture Organization's Database on Introductions of Aquatic Species).

	Number of introductions	Percentage established	<i>P</i>	Percentage causing ecological effects	<i>P</i>
<i>Oreochromis mossambicus</i>	172	85.9	<0.0005	81	0.26
<i>Cyprinus carpio</i>	124	82.0	0.91	86	0.47
<i>Oncorhynchus mykiss</i>	99	53.8	0.38	88	0.51
<i>Ctenopharyngodon idella</i>	91	11.3	0.06	60	0.71
<i>Hypophthalmichthys molitrix</i>	79	26.8	0.20	75	0.24
<i>Oreochromis niloticus</i>	78	70.2	<0.0005	75	0.25
<i>Gambusia</i> spp.	67	96.8	0.43	50	0.15
<i>Micropterus salmoides</i>	64	72.9	0.78	86	0.19
<i>Aristichthys nobilis</i>	55	19.6	0.27	80	0.48
<i>Carassius auratus</i>	54	92.3	0.63	75	0.37
<i>Lepomis gibbosus</i>	25	91.3	0.01	71	—
<i>Procambarus clarkii</i>	24	88.9	0.62	86	0.74

**Note:** The number of introductions refers to introductions to different countries. Several introductions of the same species into the same country are not considered. The *P* values correspond to *G* tests of independence of establishment or presence of ecological effects (yes/no) in different continents.

Following Williamson (1996), percentages refer to the total number of species in the previous transition, e.g., the percentage of those species which established (not of the total which were introduced) that had ecological effects. Unfortunately, the effect of introduction effort within a country cannot be analyzed because in the DIAS database, only the first introduction is given for each country.

We prepared three data sets. One contained all the world's introductions of the 10 most frequently introduced aquatic species plus 2 aquatic species regarded as very invasive in Europe, the red swamp crayfish (*Procambarus clarkii*), which is the second most frequently introduced crustacean, and the pumpkinseed sunfish (*Lepomis gibbosus*) (Keith and Allardi 1998; García-Berthou and Moreno-Amich 2000a) (Table 1). We added to this database the continent of introduction. With this data set we described the invasion rates of the different species and analyzed whether they varied with the continent of introduction and year. The second data set was a transition matrix of the total number of species introduced from one given European country to another. The countries on other continents were not specified, so pool regions (continents) were used instead. A correspondence analysis (CA) of this transition matrix (38 × 38 countries/continents) showed the pathways of introduction within Europe and the main sources of variation. For European countries we added the country's area, latitude, longitude, gross domestic product per capita (GDPC), and population density (from Central Intelligence Agency 2001) to analyze their effects on the number of introductions received and given. The third data set consisted of all introductions (264 introductions of 123 different aquatic species) to six large European countries at contrasting latitudes: United Kingdom (UK), France, Spain, Sweden, Germany, and Italy. The objective was to compare the invasibility of large countries (i.e., to partial out the effect of country size but use countries large enough to avoid low numbers of introductions) at contrasting latitudes (and

hence contrasting water availability and environmental features).

### Statistical analyses

Contingency tables were analyzed with *G* tests of independence. To test the effect of a quantitative predictor (e.g., year of introduction) on a qualitative response variable (e.g., the percentage successfully established or the percentage causing ecological effects) we used logistic regression; we considered the models both with and without categorical factors (continent). For logistic regression, we report the  $\chi^2$  value (and its associated *P* value) that compares the full model with the constant-only model, and we also report Nagelkerke's *R*<sup>2</sup>, which is similar to the ordinary determination coefficient (Tabachnick and Fidell 2001).

Multiple linear regression was used to relate the number of introductions to a country's area, latitude, and longitude. Stepwise selection procedures were used (although similar results were obtained without selection procedures). We used the square of latitude and longitude in the models to test for nonlinear, parabolic responses (i.e., polynomial regression). Latitude was centered (i.e., the mean was subtracted) before squaring it to reduce collinearity. The adjusted coefficient of determination, which corrects the overestimation due to the number of variables, is reported (Tabachnick and Fidell 2001).

Path analysis was used to better include intervening variables that may mediate between number of introductions and geographical characteristics, such as GDPC and population density. Path analysis is strongly related to regression analysis but has the following advantages: automatic computation of indirect effects, the ability to treat all equations in a single model, the ability to deal with non-recursive systems, and the availability of tests of significance of all the potentially omitted parameters. We estimated the recursive saturated model (i.e., assuming a causal order among variables and estimating all possible effects that are coherent with this order) on

the correlation matrix using the maximum-likelihood estimator for general structural equation models, as available in the program LISREL 8.54 (Du Toit and Du Toit 2001). Then, we went into a specification search process by removing one by one nonsignificant paths (with a  $t$  value lower than 2), by assessing the interpretability of the results after each modification, and by testing each time the significance of all parameters omitted in previous steps, both jointly by means of a likelihood ratio test and individually by means of Lagrange's multiplier tests, also known as modification indices. This corresponds to the model-generating strategy of structural equation modelling defined in Jöreskog (1993).

CA was used to ordinate and summarize information consisting of large contingency tables of number of introductions (species  $\times$  continent and country of origin  $\times$  country of destination). CA is similar to principal component analysis but performs better with matrices of count data with many zeros that are the norm in community ecology (Jongman et al. 1995). Transformations are generally not necessary in CA, since counts are implicitly weighted by row and column totals (usually species and sample totals). The results of CA are usually presented in separate plots or a joint plot of row and column scores for the first dimensions, which explain most of the variation. Close scores in the CA plot correspond to similar entities, and the relationship between rows and columns of the matrix is also displayed, i.e., closer species scores indicate species disproportionately introduced to a given continent (which will also have scores close to the species scores in the plot). All statistical analyses (except path analysis) were computed with SPSS version 11.5 (SPSS Inc. 2002).

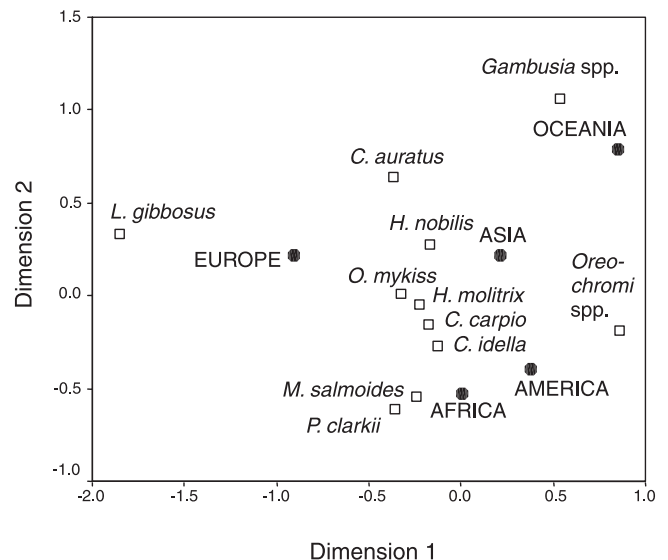
## Results

### The most frequently introduced aquatic species

According to the DIAS database, the 10 most frequently introduced aquatic species in the world are all freshwater fishes, which have been introduced into over 50 countries (Table 1). There are significant differences among continents in the introduction intensity of different species ( $G_{[40]} = 148.1$ ,  $P < 0.0005$ ) and a CA (Fig. 1) shows that the pumpkinseed sunfish has been introduced mostly to Europe, mosquitofish (*Gambusia* spp.) mostly to Oceania, tilapias (*Oreochromis* spp.) mostly to America and Oceania, the largemouth bass (*Micropterus salmoides*) mostly to Africa, and the bighead carp (*Aristichthys nobilis*) mostly to Asia. Of the 25 introductions of pumpkinseed sunfish (Table 1), 72% were to European countries; of the 172 introductions of tilapias, 34% were to America, 16% to Oceania, and only 6% to Europe; of the introductions of mosquitofish, 27% were to Oceania; of the introductions of goldfish (*Carassius auratus*), 37% were to Europe and only 7% to Africa; of the introductions of largemouth bass, 30% were to Africa and only 12% to Asia; and of the introductions of bighead carp, 40% were to Asia and only 9% to Africa.

There is also significant variation in establishment rates among continents (Table 1). Over 65% of introduced tilapias successfully established, except in Europe, where all introductions have failed. The introductions of pumpkinseed sunfish were all successful, except two out of three attempts in

**Fig. 1.** Correspondence analysis of the number of introductions, by continent, of the most frequently introduced aquatic species ( $\square$ , species scores;  $\bullet$ , continent scores). The two first dimensions explain 75.5% of the variance.



Africa and Asia. The probability of establishment is lower for the grass carp (*Ctenopharyngodon idella*), bighead carp, and silver carp (*Hypophthalmichthys molitrix*). For the tilapias there is also a saturation effect, and a logistic regression function shows that about 20% of the most recent introductions have failed (mostly in Europe) in contrast to the earliest introductions, which were all successful (Fig. 2).

Over 50% of the successful introductions of the 12 species had ecological effects, and the occurrence of ecological effects does not depend significantly on the destination continent (Table 1) or year of introduction (logistic regression,  $P \gg 0.05$ ). For these 12 species, there was no significant relationship between the number of introductions and the percentage established ( $r = -0.03$ ,  $n = 11$ ,  $P = 0.93$ ) or the percentage causing ecological effects ( $r = -0.09$ ,  $n = 11$ ,  $P = 0.79$ ).

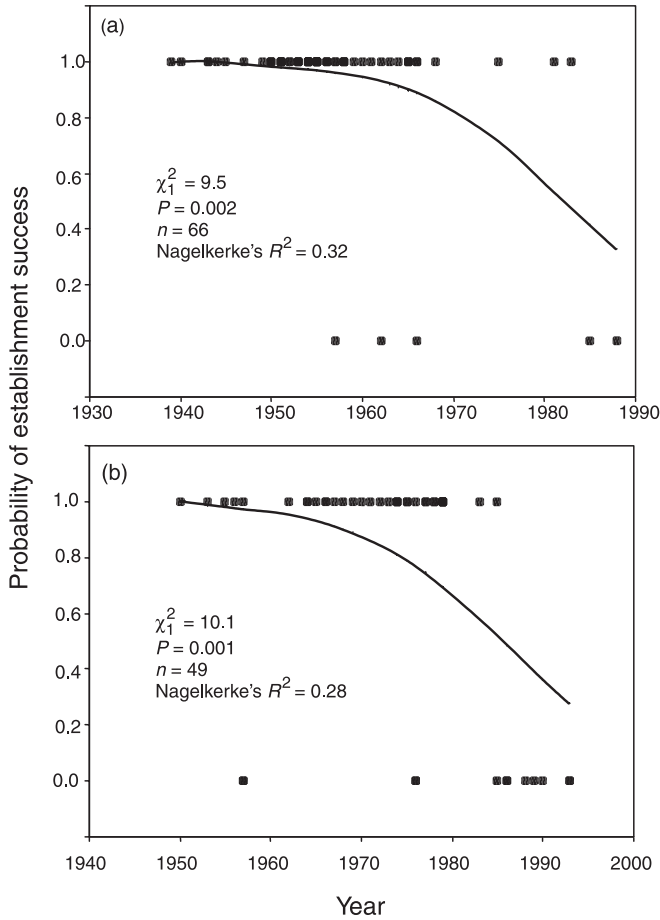
### Invasion rates in six European countries

The number of species introduced is much lower in Sweden than in the other five large countries assessed, although no significant effect of latitude was obtained with multiple regression (but see the next section). The mean percentage established of the 123 aquatic species in the six countries is above 50%, and the average is 63% (Table 2). There is some suggestion that the percentage established varies among countries ( $G_{[5]} = 10.1$ ,  $P = 0.072$ ), establishment success being lowest at higher latitudes and longitudes ( $r = -0.82$ ,  $n = 6$ ,  $P = 0.047$ ). The frequency of ecological effects does not vary significantly among countries ( $G_{[5]} = 1.6$ ,  $P = 0.12$ ) and is 69%, on average. There is no significant relationship between the number of introductions and the percentage established ( $r = 0.51$ ,  $n = 6$ ,  $P = 0.30$ ) or the percentage causing ecological effects ( $r = 0.01$ ,  $n = 6$ ,  $P = 0.98$ ).

### Introduction pathways within Europe

The first two dimensions of a CA of the transition matrix of introduction counts (38  $\times$  38 countries) explained 32.4%

**Fig. 2.** Historical variation in establishment success of tilapias, (a) *Oreochromis mossambicus* and (b) *Oreochromis niloticus*, in Europe. The data points are recorded introductions (1 = established; 0 = not established) and the line shows the probability of establishment success predicted by logistic regression.

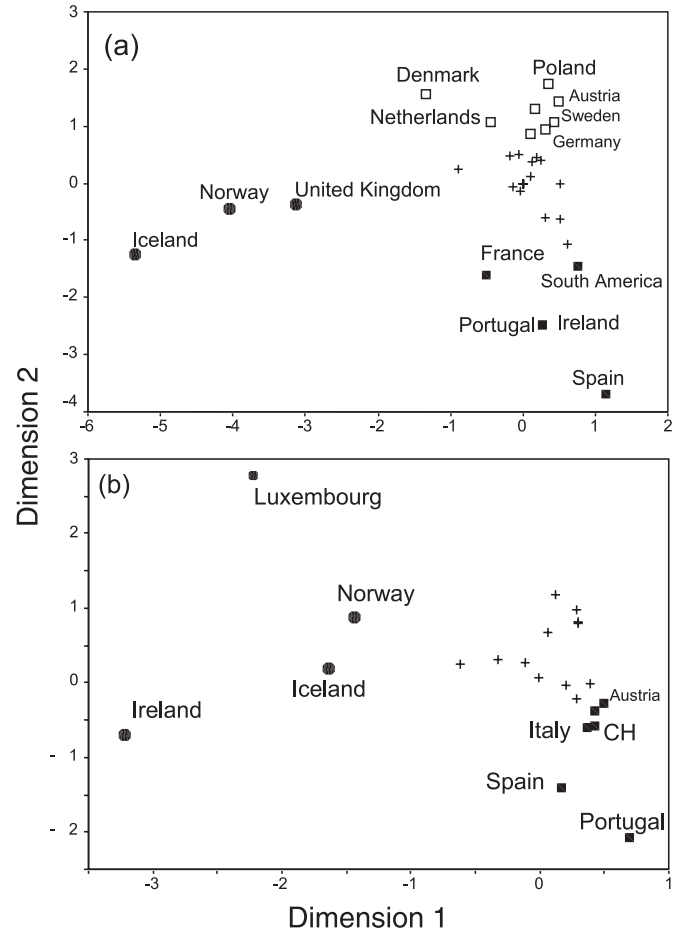


**Table 2.** Invasion transition rates in six large European countries at contrasting latitudes.

	Number of introductions	Percentage established	Percentage causing ecological effects
United Kingdom	47	62.8	80
France	63	69.5	83
Spain	42	80.0	36
Sweden	16	43.8	67
Germany	40	67.6	100
Italy	56	55.6	71

of the variation (Fig. 3). The CA summarizes introduction-pathway relationships among European countries. Three regions of origin of introductions are distinguished by *k*-means clustering from the rest of the CA origin scores (Fig. 3a): (1) northwestern European countries, dominated by the UK. The CA destination scores (Fig. 3b) distinguish Ireland as the main destination. The UK gave 14 of the total of 26 introductions to Ireland; (2) northern countries, dominated by

**Fig. 3.** Correspondence analysis of the transition matrix of introductions (number of species introduced from one country to another). Scores for (a) origin and (b) destination countries are given. Countries with different symbols are in different clusters obtained by *k*-means clustering: only the countries that are most differentiated are labelled; a plus sign (+) denotes countries with central scores (not differentiated by the dimensions). CH, Switzerland.

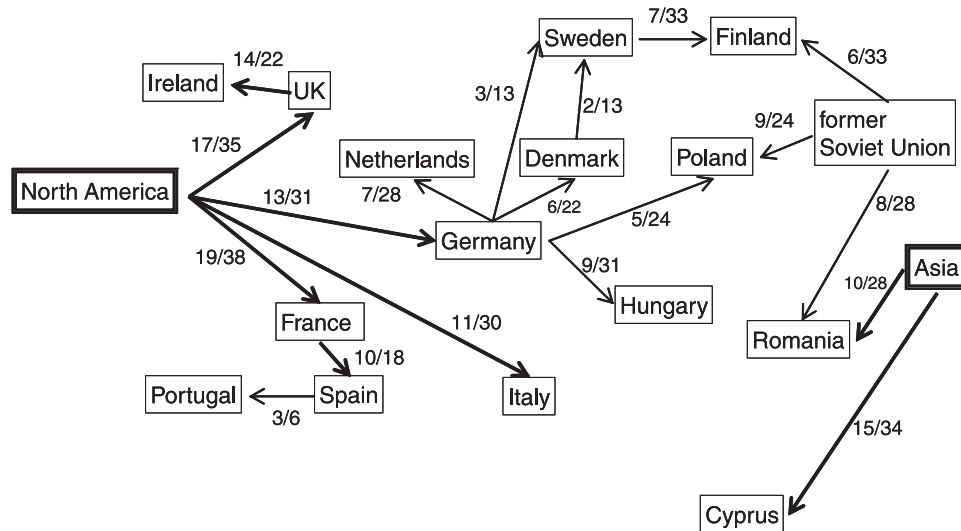


Germany, that provide species to many different countries; and (3) southwestern countries, with France as the main donor of species to Spain and Portugal.

The CA origin scores (Fig. 3a) distinguish large countries such as the UK, Germany, and France that are not distinguished among the CA destination scores (Fig. 3b). This reflects the strong asymmetry in the exchange of non-indigenous species (NIS), with strong unidirectional pathways. Of the 26 species introduced from the UK, 14 went to Ireland; in contrast, Ireland provided only one introduction (not to the UK but to Spain). Of the 18 species introduced from France, 10 went to Spain, whereas the 3 introduced from Spain went to Portugal.

There are, therefore, clear introduction pathways in Europe (Fig. 4). The many species of North American origin enter France, the UK, Germany, and Italy independently. There is strong introduction intensity from the UK to Ireland, from France to Spain, and from Spain to Portugal, illustrating “stepping stone” invasion patterns. Germany acts

**Fig. 4.** The main introduction pathways of aquatic species within Europe. The fractions denote the number of species introduced from one country to another (numerator) followed by the total number of introductions received, excluding those of unknown origin (denominator). For instance, of the 22 species of known origin introduced to Ireland, 14 (i.e., 64%) came from the United Kingdom. Relationships involving 10 or more introductions are indicated by thick arrows. Less important relationships have been omitted.



**Table 3.** Multiple linear regression models (stepwise selection procedure) of the number of introductions with country area and latitude.

Model	$R^2_{adj}$	$P$
$\log(\text{GIVEN} + 1) = -10.4 + 0.40 \log \text{AREA} - 0.38 \text{LAT} - 0.004 \text{LAT}^2$	0.31	0.017
$\log \text{RECEIVED} = -0.376 + 0.44 \log \text{AREA} - 0.0002 \text{LAT}^2$	0.48	0.001
$\log \text{RECEIVED} = -0.17 + 0.35 \log \text{AREA} + 0.23 \log(\text{GIVEN} + 1) - 0.0002 \text{LAT}^2$	0.56	<0.0005

**Note:** GIVEN is the number of species introduced from the country to other countries; RECEIVED is the number of species introduced to the country; AREA is the area of the country (km<sup>2</sup>); LAT is latitude (deg.); log is the decimal logarithm; and  $R^2_{adj}$  is the adjusted coefficient of determination ( $n = 23$  European countries). All the regression coefficients were significant ( $P < 0.05$ ).

as a source of NIS for many countries in central and eastern Europe. Besides North America, most NIS originate from Asia or the former Soviet Union and enter through Romania and Poland.

### Effects of a country's area and latitude on the number of introductions

Multiple linear regression analysis shows that the number of introductions originating from a given country is significantly and independently related both to its area and its latitude (Table 3). The standardized regression coefficients and their  $P$  values show that the parabolic latitudinal effects are more important than the country's area. Most species are introduced from midlatitude Europe and secondarily from large countries, whereas few species are introduced from either northern or southern latitudes.

The number of introductions received by a country is also related to its area and latitude (Table 3). However, area is more important here than latitude, and the latitudinal effect is monotonic, i.e., southern and central countries receive similar numbers of introductions and only Nordic countries receive fewer.

The relationship between the number of introductions received and given by a country is significant ( $P < 0.05$ ; Fig. 5) and the slope is significantly different from a 1:1 relationship ( $P < 0.05$ ) because most countries receive many

more species than they give, except for five large, rather midlatitude countries. There is a positive effect of a country's area on the ratio of received to given introductions and a quadratic effect of latitude (Table 3), and beta coefficients show that area is the most important factor in this relationship and the number of introductions given is the least important. The ratio of received to given introductions is higher in southern countries and lower in northern countries, and three types of country can be summarized (Fig. 5): "recipient and donor" countries: these give and receive many introductions, and are mainly large, rather midlatitude countries such as France, Germany, the UK, and Hungary; "recipient" countries: these give few species but receive many, and include most of the countries, although southern countries receive proportionally more species; and "neither recipient nor donor" countries (only Iceland and Luxembourg). No country is only a "donor".

### Effects of population density and GDPC

We obtained a relatively low degree of collinearity among the variables (Table 4), in part through centering latitude before squaring it, using GDPC instead of total gross domestic product, and using population per square kilometre instead of total population. All the effects shown (with arrows) in the model finally obtained (Fig. 6) were significant ( $P < 0.05$ ). The model did not significantly deviate from the ini-

**Table 4.** Correlation matrix of the variables for the 23 European countries analyzed.

	log RECEIVED <sup>a</sup>	log GIVEN <sup>b</sup>	GDPC <sup>c</sup>	Population density <sup>d</sup>	log AREA <sup>e</sup>	Latitude (deg.)	Latitude squared <sup>f</sup>
log RECEIVED <sup>a</sup>	—	0.008	0.031	0.407	0.003	0.162	0.601
log GIVEN <sup>b</sup>	0.539	—	0.801	0.065	0.071	0.838	0.026
GDPC <sup>c</sup>	-0.449	-0.056	—	0.326	0.055	0.108	0.785
Population density <sup>d</sup>	0.182	0.391	0.215	—	0.179	0.538	0.004
log AREA <sup>e</sup>	0.584	0.384	-0.405	-0.291	—	0.372	0.666
Latitude	-0.302	0.045	0.344	-0.135	0.195	—	0.300
Latitude squared <sup>f</sup>	-0.115	-0.462	0.060	-0.581	0.095	0.226	—

**Note:** Values below the diagonal are correlation coefficients; values above the diagonal are *P* values.

<sup>a</sup>log RECEIVED is the number of species introduced to the country ( $\log_{10}$  transformed).

<sup>b</sup>log GIVEN is the number of species introduced from the country to other countries ( $\log_{10}(x+1)$  transformed).

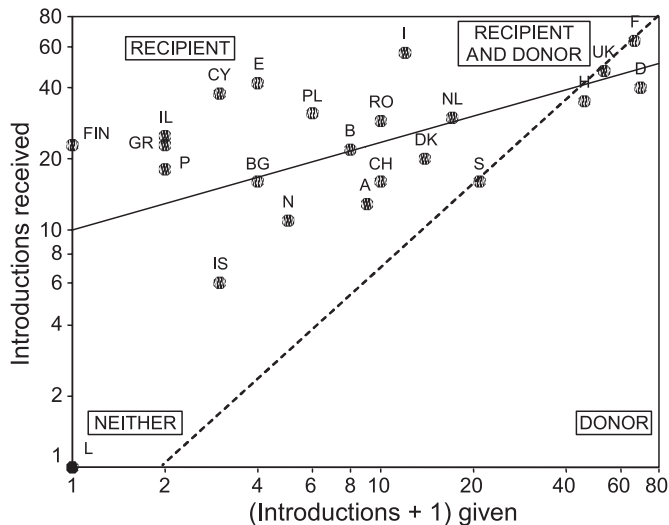
<sup>c</sup>Gross domestic product per capita (US\$).

<sup>d</sup>Number of inhabitants·km<sup>-2</sup>.

<sup>e</sup>Area of the country (km<sup>2</sup>;  $\log_{10}$  transformed).

<sup>f</sup>Previously centered.

**Fig. 5.** Relationship of the number of introductions received with the number of introductions given by European countries (A, Austria; B, Belgium; BG, Bulgaria; CH, Switzerland; CY, Cyprus; D, Germany; DK, Denmark; E, Spain; F, France; FIN, Finland; GR, Greece; H, Hungary; I, Italy; IL, Ireland; IS, Iceland; L, Luxembourg; N, Norway; NL, the Netherlands; P, Portugal; PL, Poland; RO, Romania; S, Sweden; UK, the United Kingdom). The linear regression function (solid line) and the 1:1 relationship (broken line) are also shown.



tial saturated model (likelihood ratio test = 11.9, *df* = 10, *P* = 0.29). The maximum Lagrange multiplier test for individual omitted parameters was also nonsignificant ( $\chi^2_1 = 1.9$ , *P* = 0.17) *R*<sup>2</sup> values were 0.350 for GDPC, 0.337 for population density, 0.423 for introductions given, and 0.632 for introductions received. The following points emerge from the results of path analysis (Fig. 6): (i) the country's area (the most important explanatory variable) and population density affect the numbers of species both received and given. No effect of GDPC was found; (ii) there is a direct, negative effect of latitude on the number of introductions received. In contrast, the previously observed quadratic effect of latitude on the number of introductions given is mediated by population density (countries in central Europe are the most

densely populated and give most of the introductions); (iii) when controlling for the explanatory variables, no significant relationship between the number of species given (GIVEN) and received (RECEIVED) is left, therefore the number of introductions in a country per se does not affect its exportation rate, despite the apparent correlation. No significant correlation is found between the error terms of GIVEN and RECEIVED, hence supporting their randomness and the completeness of the model.

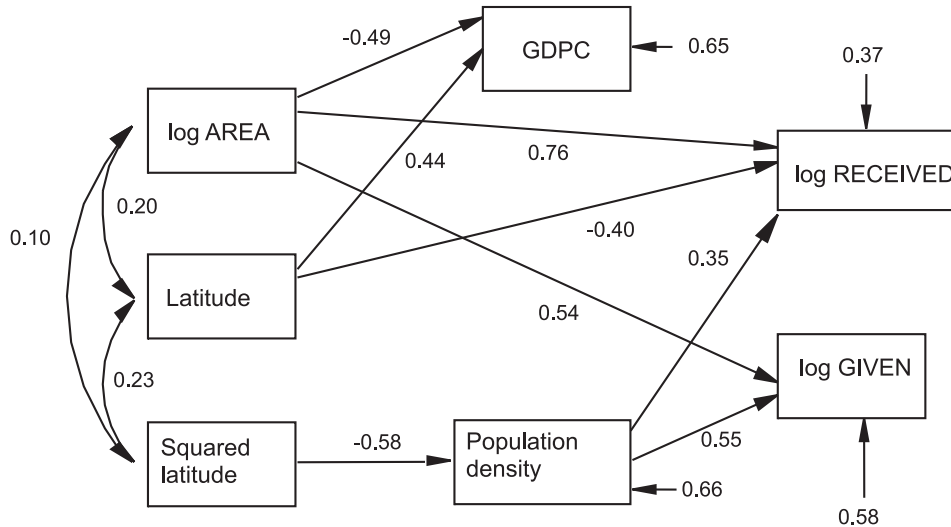
## Discussion

### Introduction pathways

There are significant differences among continents in the frequency of introductions of different species. For instance, the pumpkinseed sunfish has been introduced mostly to Europe, whereas mosquitofish are widespread in Oceania. There are also some significant intercontinental differences in establishment success but only for a few species, and establishment success is generally high and less important than the introduction effort (see the previous section). Therefore, the differential introduction frequency is mediated by historical and sociological factors rather than ecological factors. For instance, the pumpkinseed sunfish would be expected to adapt well to many African countries (there were only two introduction records in DIAS), where the largemouth bass, a species often cohabiting with the pumpkinseed sunfish in its native range, is widespread. Similarly, mosquitofish are relatively less introduced in Africa and South America but may establish successfully in many countries.

MacIsaac et al. (2001) have recently identified several indirect corridors within Europe that facilitate the invasion of the Laurentian Great Lakes by species mostly from the Ponto-Caspian region. These corridors go from the Black, Azov, and Caspian seas to the North and Baltic seas through the Danube, Dnieper, and Volga rivers (in a northwesterly direction) (Bij de Vaate et al. 2002). These corridors are not observed in our results because they referred to invertebrates (amphipods and crustaceans) with some degree of salinity tolerance and accidentally introduced through ballast water (Ricciardi and Rasmussen 1998; Ricciardi and MacIsaac 2000; MacIsaac et al. 2001), whereas most of the introduced aquatic species in Europe are fishes of freshwater habitats

**Fig. 6.** Path diagram of the final model. Standardized estimates of significant direct effects (single-headed arrows originating from a given variable) and standardized error variances ( $1 - R^2$ ; arrows not originating from variables) are shown. Variables are as follows: log RECEIVED is the number of species introduced to the country ( $\log_{10}$  transformed); log GIVEN is the number of species introduced from the country to other countries ( $\log_{10}(x + 1)$  transformed); GDPC is the gross domestic product per capita (US\$); population density is the number of inhabitants- $\text{km}^{-2}$ ; log AREA is the area of the country ( $\text{km}^2$ ;  $\log_{10}$  transformed); latitude is in degrees; the square of the latitude is previously centered.



and were intentionally introduced. This suggests the existence of two opposing pathways in Europe for intentional (freshwater fishes) and accidental introduction (euryhaline invertebrate species). In contrast to other taxa such as plants and terrestrial vertebrates, freshwater species introduced to Europe come mostly from North America (Welcomme 1991; Vilà et al. 2001) and enter through midlatitude countries in western Europe (France, the UK, and Germany) and from there go mostly to southern Europe. In contrast, the numerous Eurasian euryhaline species (mostly invertebrates but also a few fish species) that have invaded North American waters come from the Ponto-Caspian region through northern Europe, invading Europe in a northwesterly direction.

The species richness – area relationship is one of the main topics of ecology and a pervasive pattern at all scales. It is also observed with the number of aquatic NIS introduced in Europe. Interestingly, the numbers of introductions received (RECEIVED) and given (GIVEN) by a country are mediated by different mechanisms: RECEIVED depends mostly on country area and secondarily on latitude, whereas GIVEN depends on population density and area. For RECEIVED, area is a synthetic measure of the diversity of habitats and ecosystems available and the number of river basins (where independent introductions are carried out for freshwater fishes). In contrast, the country of origin (GIVEN) depends mostly on population density and this factor explains the quadratic effect of latitude. For worldwide (received) introductions of terrestrial plants, Dalmazzone (2000) also found that population density was more important than GDPC, but she found some significant effects of GDPC, which is more logical for species accidentally introduced by passive transport, such as most terrestrial plants. The differential influences of GDPC versus population density on passively versus actively transported invasive species should be tested further; they might work as indicators of propagule pressure.

#### Invasion transition rates

Our results show that the establishment rates of aquatic species in Europe, at least for freshwater fishes, deviate from Williamson's tens rule. The percentage established of the 123 aquatic species in six contrasting European countries is, on average, 63% (167 of 264). This figure might be biased, owing to unrecorded unsuccessful introductions. However, the bias seems unlikely to be great enough to fit within the 5%–20% range that would be expected according to Williamson's tens rule, at least for freshwater fishes. We would need some additional 571–3076 unrecorded, unsuccessfully introduced species, or even more, because there are also many established NIS that are not recorded in DIAS. Williamson and co-authors (Williamson 1996; Williamson and Fitter 1996) report several cases that justify the tens rule and some examples that deviate from it, but not freshwater fishes. Our results confirm that intentional introductions (such as previously shown with edible crop plants and biological control) would be expected to have establishment success over 20%, on average.

Most of the 10 most frequently introduced species in the world have establishment success (70%–97%) above the average, but a few, such as the grass carp (11%), bighead carp (20%), and silver carp (27%), display much lower success because of strict breeding requirements that usually impede their naturalization (Lever 1996). These establishment rates below the average of aquatic species in six European countries (63%), combined with the high introduction rates of these three species, confirm the importance of propagule pressure, particularly in intentionally introduced species (Mack 1996; Williamson 1996; Kolar and Lodge 2001). Additionally, the correlations between number of introductions and establishment success were very low and clearly nonsignificant both among species and among countries. Therefore, the two invasion transitions are quite independent (see also Kolar and Lodge 2001, 2002) and the introduction transition is more decisive than the estab-

lishment one, i.e., widely established species become so not because of a better establishment capability but because their introduction was attempted in many countries.

We did not evaluate the first 10 of the tens rule, i.e., that about 10% of the imported species are introduced to the wild, because no data were available. Too few data are available on this first transition (Williamson 1996; Williamson and Fitter 1996) to call it a rule, but it seems likely that aquatic species in Europe, or at least freshwater fishes, also deviate from 10% but in the opposite direction. The number of aquatic species recorded as having been introduced (successfully or not) in the wild in six large European countries was 123 in total (with a maximum of 65 in a single country), and the number of imported species should be between 615 and 2460 (or below 1300 for a single country) to fit the first of the tens rules. In contrast, it has been estimated that many thousand species of freshwater, brackish water, and marine protists, plants, and animals are transported at any moment in the ballast water of ships (Carlton and Geller 1993). The Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) regulates the world traffic of more than 30 000 species of animals and plants that are threatened or nearly so. There are about 25 000 fish species and many more aquatic invertebrates; popular atlases of aquarium fish (likely to be regularly imported to Europe) contain over 800 species. Therefore, many thousands of aquatic species are likely imported to Europe every year and a very small selection of them are introduced (intentionally or not) to the wild.

The occurrence of ecological effects caused by NIS was 69%, on average. All the most frequently introduced species were more likely to produce ecological effects except the grass carp and the mosquitofish. The lowest percentage for mosquitofish is unconvincing because their potential ecological impact is well known (Meffe and Snelson 1989; Arthington 1991); this pattern might be due to their smaller size and the difficulty of detecting their predation on small fish, eggs, and other organisms (Nesbit and Meffe 1993; García-Berthou 1999) or to bias in the DIAS database with this transition (see Methods). Although strong ecological impacts are characteristic of introduced freshwater fishes (Williamson 1996), it has not been reported that they display such high percentages of establishment and ecological effects. In a review by the US Congress Office of Technology Assessment (1993), the percentage of harmful NIS in the USA ranged between 4% and 19% and was lowest for fishes (4/111) and highest for terrestrial vertebrates and molluscs, but this corresponds to Williamson's pest transition.

### Management implications

We have identified clear introduction pathways of aquatic species into Europe that have profound management implications. Introductions of new species to European countries start in large, central Europe countries; from there they proceed to southern and, secondarily, northern latitudes. Further introduction pathways were identified that highlight where prevention efforts should be concentrated, e.g., most species introduced to Spain come from southern France (see also García-Berthou and Moreno-Amich 2000b), most species introduced to Portugal come from western Spain, etc. Species

already introduced to the usual country donor should be of most concern (MacIsaac et al. 2001) because they will be the "next" introduction and prevention plans should be in place (e.g., their transport should be effectively banned) and the first introductions should be eradicated, if this is feasible, before the invasion becomes irreversible. Most of these introductions are illegal nowadays and the pathways show the entry routes where more control should be implemented.

Introduction prevention should be regulated at all organizational levels; because the establishment transition is less crucial than the introduction one, it is essential to avoid the introduction of new species to new continents. Because illegal or accidental introductions to new countries within a continent (or new basins within a country) are difficult to avoid, legislation and implementation should be internationally coordinated. Previous success and, to a lesser extent, taxonomy are relatively good predictors of invasive potential (Mack 1996; Williamson 1999), and species and families with previous invasive histories should be of special concern. For terrestrial plants, it has been shown that it is probably more efficient to control new, nascent foci than the main area invaded (Moody and Mack 1998).

Regression analysis allows the identification of three types of country: recipient and donor, recipient, and neither recipient nor donor. The recipient and donor type comprises four countries where the exchange of new NIS is more intense and should be more controlled. From a conservation point of view, it is of concern that southern countries, which within Europe contain a higher proportion of endemic fishes (Almaça 1995; Bianco 1995; Elvira 1995), are among the countries that receive more NIS (recipients). Given the lower availability of water in southern Europe and the higher number of endemics, a stronger ecological impact of NIS seems likely. In contrast, northern Europe has a lower number of native and endemic species and also a lower number of NIS. This pattern is similar to that in the United States, where states with fewer native species considered desirable gamefish (the western states and New England) have received more NIS (Rahel 2000). The control and survey of fish NIS is an urgent need, particularly in southern Europe. We know very little about the ecological impact of most introduced species (Blossey 1999; Parker et al. 1999; Ruiz et al. 1999), including freshwater fishes (Keith and Allardi 1998; García-Berthou and Moreno-Amich 2000b; Crivelli 2002), and more funds, attention, and long-term monitoring should be devoted to this important environmental problem.

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