

The characteristics of invasive fishes: what has been learned so far?

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Invasive species are increasingly recognized as one of the main threats to biodiversity and both an urgent need and a unique tool for ecological research. Although attempts to identify future invasive species are not new to ecology, rigorous quantitative analyses emanate mostly from the last decade. In 2001, quantitative studies dealing with the distinguishing ecological features of invasive species were reviewed but no papers on fish species were identified. Subsequently, several quantitative studies have addressed this issue for freshwater fishes, including those that have focused on California, Colorado, the Great Lakes of North America and the Iberian Peninsula. In the present paper, 12 such studies are reviewed and compared with regard to their conclusions and methodology. The issues of different invasion stages and comparison strategies, propagule pressure, information-theoretic analyses *v.* sequential techniques, use of phylogenetic comparative methods and spatial scale are discussed. Non-native fish transport and release are the least investigated although taxonomy and human interests seem key in these first initial stages. Establishment success, which has received more study, seems more multi-factorial, context-dependent and more mediated by species-specific life-history traits. The dispersal and impact phases are less understood, although the comparison of traits (and taxonomy) between native and invasive species and particularly its variability holds promise. The lack of data on propagule pressure and the use of sequential techniques for observational data sets with many intercorrelated variables could affect the conclusions of previous studies. Research on the dispersal, impact and particularly transport and introduction phases should be prioritized rather than establishment. All the studies identified were at temperate latitudes in the northern hemisphere; studies in other regions and comparison of different regions and multiple scales are lacking.

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INTRODUCTION

Invasive species, *i.e.* non-native species that spread beyond the introduction site and become abundant (Rejmánek *et al.*, 2002), are increasingly recognized as one of the main threats to biodiversity and one of the main drivers of global change. Human domination of the Earth's ecosystems and the recent increases in transport capacity and economic globalization have accelerated the rate of

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introduction of non-native (or non-indigenous or exotic) species (Vitousek *et al.*, 1997; Kolar & Lodge, 2001; Rahel, 2002). This is leading to worldwide biotic homogenization through the establishment of non-native species, often widespread elsewhere and tolerant of degraded habitats, and the extinction of native or endemic species (Rahel, 2002; Olden *et al.*, 2004a; Clavero & García-Berthou, 2005). Freshwater ecosystems and fish taxa are particularly affected by introductions (Marchetti *et al.*, 2004a; Clavero & García-Berthou, 2006). The two classical examples are the apparent extinction of *c.* 200 species of haplochromines following the introduction of Nile perch *Lates niloticus* L. into Lake Victoria and the profound alteration of the Laurentian Great Lakes ecosystems by zebra mussel *Dreissena polymorpha* (Pallas) and other introduced species (Williamson, 1996; Balirwa *et al.*, 2003). The economic costs of these invasive species are also enormous (Pimentel *et al.*, 2000, 2005).

Understanding the factors leading to successful invasions is of great practical and conceptual importance. From a practical point of view, it should help to prevent future invasions and to mitigate the effects of recent invaders through early detection and the prioritization of management measures. Conceptually, these are 'experiments in nature', which provide unique opportunities to test ecological theories at unusual spatial and temporal scales (Gaston & Blackburn, 1999; Sax, 2001; Rice & Sax, 2005). Although trying to identify the traits of invasive species and future invaders has a long history in ecology (Ehrlich, 1989; Williamson, 1996), rigorous quantitative analyses are mostly from the last decade (Kolar & Lodge, 2001). For instance, the seminal paper by Kolar & Lodge (2001) reviewed quantitative studies dealing with the distinguishing ecological features of invasive species. Their subsequent study (Kolar & Lodge, 2002) was probably the first attempt for fish species, despite fishes being known to have remarkable ecological impacts in some cases. Several subsequent studies, however, have addressed this issue for freshwater fishes, including studies focusing on California, Colorado, the Great Lakes of North America and the Iberian Peninsula. An electronic survey of papers in the last 46 years (Fig. 1) clearly shows that: (1) the proportion of papers using the term 'invasive species' instead of 'introduced species' has recently increased, probably showing inconsistent changes in terminology that should be considered in literature searches, (2) that before 1990, only *c.* 14 papers that used 'introduced fish' or similar combinations in the title had been published and (3) that the literature on invasive species has 'exploded' mostly in the last 10 years, particularly for plants but also fishes.

The aim of the present paper was to review and compare the quantitative studies on invasive fishes with regard to their conclusions and methodological approaches. Similar to Kolar & Lodge (2001), the current paper considered only those papers that quantitatively analysed the characteristics of invasive fishes, including life-history traits, in any phase of the invasion process beyond simply taxonomy and the recipient region. These approaches are expected to have more general predictive power than those that merely consider the previous invasive success of particular species. Therefore, excluded from this review are the following types of study: (1) the purely theoretical or review papers that suggest traits of invasive fishes but without quantitative analyses (Moyle & Light, 1996; Ricciardi & Rasmussen, 1998), (2) a few studies comparing native

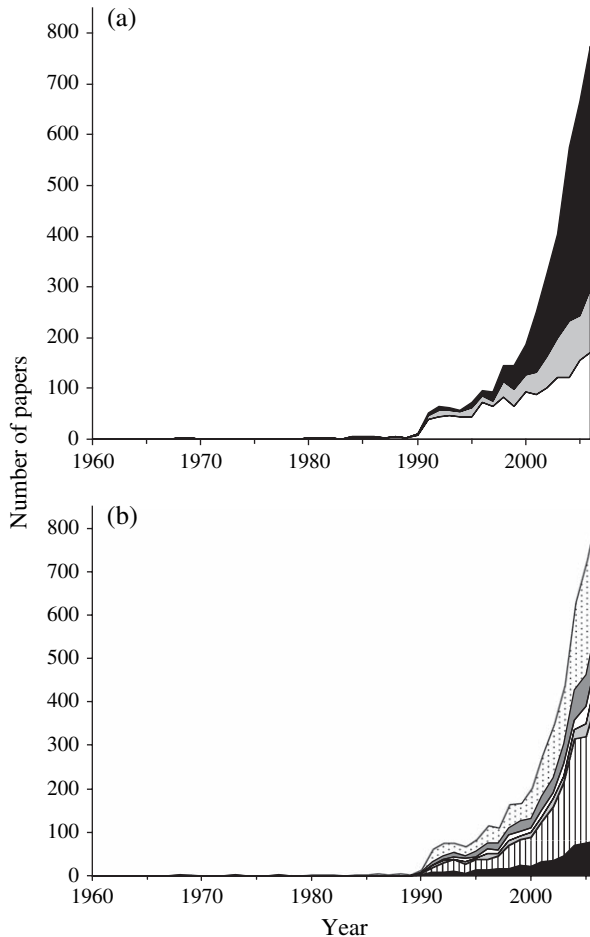


FIG. 1. Trends in the study of invasive species from 1960 to 2006 according to the ISI Web of ScienceSM Science Citation Index Expanded database (searched February 2007). (a) Number of papers using the terms 'invasive species' (■), 'alien species' (◐), and 'introduced species' (□) in the title or the abstract by year of publication. (b) Number of the papers from (a) also using 'fish' (■), 'plant' (□), 'mollusc' (or snail or 'bivalv*') (◐), 'bird' (◑) and 'mammal' (▨). The total here is higher than in (a) because some papers cited multiple taxa (*e.g.* fishes and mollusc; ◑, others). Terms searched ended with '*' to include plurals or very similar terms. Searches did not include the terms 'exotic fish' or 'introduced fish' because multiple similar terms were used simultaneously. ISI started to include the abstracts of papers in 1990, hence affecting the probability of detecting papers.

and introduced species in only specific sites and not entire river basins or regions and (3) studies that analysed invasions phases (*e.g.* establishment rates) for different species or regions but without considering life-history traits (Marchetti *et al.*, 2004b; Ricciardi & Atkinson, 2004; García-Berthou *et al.*, 2005; Casal, 2006; Ricciardi & Mottiar, 2006), including the emerging field of ecological niche modelling (Iguchi *et al.*, 2004; Zambrano *et al.*, 2006), which is based on environmental characteristics of sites only.

WHAT TO COMPARE?

Biological invasions are complex processes that consist of a sequence of phases: transport to a new region, release or escapement to the wild, establishment, dispersal or spread and integration or impact (Williamson, 1996; Kolar & Lodge, 2001; Sakai *et al.*, 2001). Each phase should be studied independently because different factors are mediating each phase and a characteristic that enhances a specific phase may compromise success in the next one (Kolar & Lodge, 2001, 2002; Cassey *et al.*, 2004a; Jeschke & Strayer, 2006). In principle, to identify the traits that determine success in a specific invasion stage, the species pools to be compared should be carefully specified, in order to avoid potentially incorrect conclusions (Cassey *et al.*, 2004b). For instance, species introduced and successfully established in a region should not be compared with the pool of species potentially introduced, or with those transported (introduced or not), but they can be compared with species introduced to the wild but not established. Otherwise, the traits involved in establishment success might be confounded with those involved in transport and introduction (Cassey *et al.*, 2004b). The transport and introduction phases, however, are transitory and often poorly documented. For instance, failed introductions of many species are rarely recorded, so the data are usually unavailable or strongly biased (Kolar & Lodge, 2001; García-Berthou *et al.*, 2005).

This is very much the case for fishes, as studies that carefully document the transport and release to the wild of non-native species are lacking in most cases, and the only comparison possible is by merging several invasion phases. Of the 12 studies on invasive fishes that were identified, none have specifically examined the transport phase, only three the release or escapement phase (hereafter 'introduction'), and several compared species established with species pools of other invasion stages. Nevertheless, as Cassey *et al.* (2004b) acknowledged, these latter comparisons are not necessarily invalid and may be the only possibility when no other data are available. Moreover, one may argue that such comparisons answer different questions. For example, when Jeschke & Strayer (2006) compare North American and European species introduced that have established and spread with those that have not been introduced or were introduced but failed to establish or spread, they are not examining only the dispersal phase but rather attempting to identify the traits of successfully established species relative to those that failed in any given step. The results may be more ambiguous, but they are more general and could benefit from increased sample size.

A similar general comparison is that of native species with established non-native species (the three studies with 'E/I' label in Table I). When the traits of established species (only species that succeeded the transport, release and establishment phases) and those of native species are compared, a mixture of invasion stages is examined, including the abiotic and biotic (*i.e.* relationship with native species) 'filters' of establishment and integration. Olden *et al.* (2006) have recently exemplified the enormous potential of this approach in explaining different and more variable ecological niches of invasive fishes compared to native fishes. Similarly, there are numerous studies documenting how different traits of native and exotic plants affect individual animal species and these

TABLE I. Studies examining the life-history traits of invasive fishes. Predictor variables are generally (when detailed by the authors) expressed as positively associated to success in the invasion phase. Predictors significant with univariate methods but not selected with multivariate methods were not included

Phase	Region	Species pool and number	Species groups compared (or variable analysed)	Main predictors identified	Reference
T/R	Nevada (U.S.A.)	163 extant salmonid species or sub-species (worldwide)	16 sub-species (representing 13 species) introduced to Nevada v. 147 species not introduced	Genus, maximum size	6
T/R	Europe and North America	220 species native to Europe but not to North America; 713 species native to North America and not to Europe	European species introduced to North America v. those not introduced; North American species introduced to Europe v. not introduced	Human affiliation, parental care, egg diameter, latitudinal range	7
R	North America	308 taxa sold in aquarium stores	Introduced v. not introduced	Availability in stores, fish size, taxonomic family	10
E	Great Lakes of North America	45 species introduced to the Great Lakes	Established v. not established	Relative growth, diet breadth, temperature and salinity tolerances, history of invasion	1
E	California (U.S.A.)	87 species introduced to California	Established v. not established	All the variables analysed: maximum size, size of native range, physiological tolerance, adult trophic status, propagule pressure, distance to native source, parental care, prior invasion success	3

TABLE I. Continued

Phase	Region	Species pool and number	Species groups compared (or variable analysed)	Main predictors identified	Reference
E	California (U.S.A.)	87 species introduced to California	Established v. not established	Maximum life span, physiological tolerance, smaller size of native range, propagule pressure, parental care, prior invasion success	4
E	Nevada (U.S.A.)	16 salmonid species or sub-species introduced to Nevada	Established v. not established	Propagule pressure (events and individuals), latitudinal range, latitudinal midpoint	6
E	Worldwide	1424 intentionally introduced species	Established v. not established	Taxonomic family or small size, omnivory, endemism of the recipient country, intentional establishment (introduction purpose)	8
E	North America	94 aquarium freshwater species introduced	Introduced v. established	Fish size, taxonomic family	10
E	Iberian Peninsula	35 species introduced to the Iberian Peninsula	Established v. not established	Prior invasion success, small adult size and reduced distance from native source	12
E/D	Europe and North America	14 European species introduced to North America; 35 North American species introduced to Europe	Established and dispersed v. introduced but not established or not dispersed	Parental care, fecundity, offspring per year	7

TABLE I. Continued

Phase	Region	Species pool and number	Species groups compared (or variable analysed)	Main predictors identified	Reference
T/R/E	Nevada (U.S.A.)	163 extant salmonid species or sub-species (worldwide)	Established to Nevada <i>v.</i> not established to Nevada <i>v.</i> not introduced	Maximum size and mass, latitudinal range, latitudinal midpoint	6
T/R/E/D	Europe and North America	220 plus 713 species as above	Established and dispersed <i>v.</i> not introduced or introduced but failed to establish or disperse	Propagule pressure, egg diameter	7
D	Great Lakes of North America	17 species introduced and established to the Great Lakes	Fast <i>v.</i> slow dispersal	Slow relative growth rate, temperature tolerance	1
D	California (U.S.A.)	71 species introduced or translocated to California and established	Dispersal (number of catchments)	Physiological tolerance, propagule pressure	3
D	California (U.S.A.)	71 species introduced or translocated to California and established	Dispersal (number of catchments)	Maximum life span, distance to native source, adult trophic status, prior invasion success	4
D	Colorado river basin (U.S.A.)	47 species introduced to the lower Colorado river	Dispersal (km year ⁻¹)	Equilibrium and equilibrium-opportunist specialists from Winemiller–Rose life-history model	11
D	Catalonia (north-east Spain)	22 species introduced to Catalonia	Dispersal (river length occupied, occurrence)	Introduction date	9
D	Iberian Peninsula	22 species established to the Iberian Peninsula	Dispersal (number of catchments)	Small native range, low parental care, large adult size, prior invasion success, detritivory	12

TABLE I. Continued

Phase	Region	Species pool and number	Species groups compared (or variable analysed)	Main predictors identified	Reference
I	California (U.S.A.)	71 species introduced or translocated to California and established	Species' qualitative abundance in catchments where it has established (1–5 scale)	Prior invasion success, human interest	3
I	California (U.S.A.)	71 species introduced or translocated to California and established	Qualitative abundance (1–5 scale)	Maximum size, physiological tolerance, distance to native source, adult trophic status, prior invasion success	4
I	Worldwide	254 established introduced species	With or without ecological impact	Endemism of the recipient country, introduction date	2
I	Great Lakes of North America	23 species introduced and established to the Great Lakes	Nuisance v. non-nuisance species	Small eggs, salinity tolerances	1
I	Iberian Peninsula	22 species established to the Iberian Peninsula	Dispersal (number of catchments)	Small native range, not omnivore, physiological tolerance, prior invasion success	12
E/I	Iberian Peninsula	45 species native and 24 established introduced to the Iberian Peninsula	Native v. established species	Taxonomy, latitudinal range, reproductive season, more diverse life-history traits, human affiliation	5
E/I	Catalonia (north-east Spain)	Eight native species and 22 established introduced (seven translocated and 15 foreign) to Catalonia	Native v. foreign v. translocated	Fecundity, age at maturity, maximum life span, water quality flexibility, tolerance to pollution, lower reaches habitat	9

TABLE I. Continued

Phase	Region	Species pool and number	Species groups compared (or variable analysed)	Main predictors identified	Reference
E/I	Colorado River basin (U.S.A.)	28 native species and 62 established introduced to Colorado River	Native v. established	Life-history traits favourable for (human-induced) regulated flows, more extreme and diverse suites of life-history traits (Winemiller–Rose model)	11

T, transport to a new region; R, release or escapement to the wild; E, establishment; D, dispersal; I, integration or impact.

1, Kolar & Lodge (2002); 2, Ruesink (2003); 3, Marchetti *et al.* (2004c); 4, Marchetti *et al.* (2004a); 5, Alcaraz *et al.* (2005); 6, Colautti (2005); 7, Jeschke & Strayer (2005, 2006); 8, Ruesink (2005); 9, Vila-Gispert *et al.* (2005); 10, Duggan *et al.* (2006); 11, Olden *et al.* (2006); 12, Ribeiro *et al.* (2007).

comparisons have enormous potential for predicting severe impacts (Levine *et al.*, 2003).

The operational definition of the different invasion states is another problem (Richardson *et al.*, 2000; Rejmánek *et al.*, 2002; Copp *et al.*, 2005). For instance, when should an introduced fish be considered as established or not, particularly given the long life span of some fishes, the difficulty of sampling large rivers and reservoirs, and the repeated stocking of some species? It is uncertain whether very recent introductions will establish and how to define 'recent' is subjective. Therefore, the date of introduction or the time since introduction (when known) should probably be used in statistical analyses of establishment and dispersal (Alcaraz *et al.*, 2005; García-Berthou *et al.*, 2005); otherwise, discarding 'recent introductions' might also bias the results because changing trends have been documented in the species introduced (Clavero & García-Berthou, 2006) and establishment rates (García-Berthou *et al.*, 2005; Copp *et al.*, 2007). Moreover, some establishments are very restricted in space or environmental conditions (Copp *et al.*, 2005), *e.g.* mosquitofish *Gambusia holbrooki* Girard in a Hungarian natural thermal lake (Specziár, 2004) or tropical species such as guppy *Poecilia reticulata* Peters in a Spanish thermal spring (Alcaraz *et al.*, 2005) or for a period in the 1960s–1970s in a few English water courses artificially heated by power-plant discharges (Lever, 1996). Similar problems with definitions can be found for 'spread' and 'introduction to the wild', *e.g.* for introductions to a human-made isolated pond (Copp *et al.*, 2005). Ideally, the data should also include introductions from within a region, *i.e.* native species translocated outside their native range (Marchetti *et al.*, 2004c; Vila-Gispert *et al.*, 2005) have shown that translocated species can show different life-history patterns from both native and alien species.

HOW TO COMPARE?

The statistical methods used to identify the traits of invasive species are also very diverse, ranging from univariate methods such as independence tests (for categorical predictors) or ANOVAs to multivariate methods such as logistic regression or classification trees (Table II). Univariate and multivariate methods seem clearly complementary (Cassey *et al.*, 2004a). Whereas multivariate methods take in some account the intercorrelation of variables and may be more powerful in many cases, data are often missing for some variables, which reduces the sample size and statistical power of multivariate methods (Jeschke & Strayer, 2006). Among multivariate methods for categorical dependent variables (*i.e.* excluding multiple linear regression), the main three methods that have been used for fishes (Table II) are multiple logistic regression (*i.e.* generalized linear model with binomial errors), discriminant function analysis and classification trees. Although classification trees have only been used in two studies, there is ample consensus that they are particularly suited to the analysis of complex ecological data, which may include lack of balance, missing values, non-linear relationships between variables and high-order interactions (De'ath & Fabricius, 2000; Karels *et al.*, 2004; Turgeon & Rodríguez, 2005) although this is disputed by Thuiller *et al.* (2003). For instance, Olden &

TABLE II. Methodological details of the studies identified in Table I (see Table I for abbreviation and references)

Reference	Number of predictors analysed	Measure of propagule pressure	Statistical methods used	Model selection for multivariate methods	Phylogenetic method	Geographical variation/spatial scale
1	27	Genus and species histories of introductions (y/n)	ANOVAs, CT, DFA	Stepwise procedure for DFA?	Grafen's (1989) method (family ranking variable added to the model) Independent contrasts	No
2	8	Intentional introduction and introduction date	LO, MLR	Backward procedure?		Fish richness (residual) and endemism percentage of the recipient country; difference in latitude between origin and recipient countries Used distance to nearest native source
3	8	Number of countries with introductions and the estimated number of fishes used in introductions (four categories)	LO, MLR	Information-theoretical approach	None	
4	10	Number of countries with introductions and the estimated number of fish used in introductions (four categories)	LO, MLR	Stepwise procedure based on AIC	None	Used distance to nearest native source

TABLE II. Continued

Reference	Number of predictors analysed	Measure of propagule pressure	Statistical methods used	Model selection for multivariate methods	Phylogenetic method	Geographical variation/spatial scale
5	26	Introduction purpose	<i>t</i> -tests, Levene tests, independence tests, DFA	Stepwise procedure	Independent contrasts	Comparison with a sub-region (from Vila-Gispert <i>et al.</i> , 2005)
6	10	Number of introduction events and number of propagules introduced or transported	Independence tests, ANOVAs	None	None (genera compared)	No
7	20	Number of countries or regions in which the species has been introduced	Univariate analyses, LO, MLR, estimation of effect sizes	Stepwise procedure	Independent contrasts	Comparison of Europe and North America
8	8	Intentional establishment (introduction purpose) and introduction date	CT, LO	Information-theoretic approach	None (family studied)	Fish richness (residual) and endemism percentage of the recipient country; difference in latitude between origin and recipient countries

TABLE II. Continued

Reference	Number of predictors analysed	Measure of propagule pressure	Statistical methods used	Model selection for multivariate methods	Phylogenetic method	Geographical variation/spatial scale
9	14	Introduction date	AN(C)OVAs, independence tests, DFA	Stepwise procedure	None	No
10	3	Occurrence in aquarium stores	Independence tests	Not applicable	None (taxonomic family studied)	No
11	22	None	Principal co-ordinate analysis plus <i>t</i> -tests	Not applicable	Grafen's (1989) method plus Mantel tests	Analysed native species' rate of distributional decline
12	11	Estimated number of fish used in introductions (four categories)	LO, MLR	Stepwise procedure	None	No

AIC, Akaike information criterion; CT, classification trees; DFA, discriminant function analysis; LO, multiple logistic regression; MLR, multiple linear regression.

Jackson (2002) compared these three techniques plus artificial neural networks and suggested that classification trees and neural networks greatly outperformed traditional techniques when applied to non-linear ecological data.

Within the multivariate methods, two approaches of model selection have been used: automatic, sequential techniques such as stepwise or backward procedures and, more recently, information theoretic (IT) analyses based on Akaike's information criterion (AIC) or similar extensions (Burnham & Anderson, 2002). Sequential techniques, such as stepwise selection or minimum adequate modelling, MAM (Crawley, 2002), have many flaws, mainly due to multicollinearity amongst predictors. They have received the following critiques (Thompson, 1995; Mac Nally, 2000; Burnham & Anderson, 2002; Whittingham *et al.*, 2006): the model with highest conventional or adjusted R^2 is not guaranteed to be found; the model may select unrelated predictors with good explanatory power because of their correlation with true causal variables; the results are often inconsistent, depending on the procedures used, and will produce biases in the parameter estimates; there is an inappropriate focus on a single best model. As elsewhere in ecology and behaviour, sequential techniques such as stepwise selection have been the norm for invasive fishes (Table II), either used in multiple linear regression, multiple logistic regression or discriminant function analyses. Ruesink (2005) and particularly Marchetti *et al.* (2004b) led the way for invasive fishes and exemplified the early use of IT analyses, the acknowledgement that there is not a simple 'true model' in the biological sciences (Burnham & Anderson, 2002) and the relative importance of different variables. Although Stephens *et al.* (2005) called for a pluralistic view that includes IT analyses and null-hypothesis testing as valid tools for the ecologist, they also concluded that IT analyses are better suited for observational studies that assess multivariate causality, which is clearly the case for studies reviewed here. Whittingham *et al.* (2006) suggested the use of IT analyses, or sometimes the fitting of the 'full model' (*i.e.* contains all the predictors), rather than the use of sequential techniques such as stepwise selection or MAM. The emphasis on effect sizes, instead of P values, by Jeschke & Strayer (2006) is also a good practice.

A caveat related to model selection is the contrasting total number of predictor variables tested in the different studies, which ranged from three to 27 (Table II). It is not known whether different predictors of invasiveness were identified in the different studies because of true region-specific differences or because some variables were not considered in specific studies. Of course, comprehensive data sets with numerous variables should be assembled whenever possible. The use of information theoretic approaches seems more imperative in these cases of large number of predictors.

Another interesting approach is to analyse variability as well as central tendency. Although inference is more difficult for variances than it is for means (Stewart-Oaten & Bence, 2001), two studies have shown that invasive fish species differ from native species through greater variability (Alcaraz *et al.*, 2005; Olden *et al.*, 2006), the former displaying more diverse life-history traits and being from more diverse taxonomic groups than the latter. This is to be expected since most fish introductions are now intentional (and illegal), often with the temerarious (and indeed ill-conceived) idea of 'filling vacant niches'

(e.g. fishes smaller or larger than native species) but producing unexpected consequences (Moyle & Light, 1996).

Phylogenetic comparative methods (PCMs) such as Felsenstein's independent contrasts are widely used to control for the lack of statistical independence among species. Only four of the 12 studies reviewed have used some sort of PCM (Table II). The results of phylogenetic analyses and interspecific (non-phylogenetic) comparisons can be quite different (Jeschke & Strayer, 2006), and phylogenetic analyses sometimes transform results from non-significant to significant (Rees, 1995; Alcaraz *et al.*, 2005), although the opposite is generally the rule (Garland *et al.*, 1999). Recently, there has been considerable discussion about whether PCMs should be used as regularly as they have been, but the vast literature is beyond the scope of this review (Westoby *et al.*, 1995; Mazer, 1998; Freckleton *et al.*, 2002; Martins *et al.*, 2002). Note, however, that: (1) phylogenetic dependence exists within a wide range of phylogenies and data (Freckleton *et al.*, 2002), (2) methods have recently been developed to measure the amount of phylogenetic correlation and correct only for it (Freckleton *et al.*, 2002; Blomberg *et al.*, 2003), (3) correlations estimated without taking phylogeny into account are often quite poor, and most PCMs perform quite well even when their assumptions are violated (Martins *et al.*, 2002), (4) conventional and independent contrasts correlations are often similar and correlated at $c. r = 0.85$ according to Garland *et al.* (1999), whereas statistical significance differed in 16% of cases reviewed by Freckleton *et al.* (2002), (5) some authors suggest that comparing the results of PCMs and non-phylogenetic analyses can be informative (Mazer, 1998; Garland *et al.*, 1999) but not other authors (Freckleton *et al.*, 2002) and (6) contrary to common wisdom, PCMs should not be interpreted as removing the confounding effects of phylogeny but rather as reducing the variance of estimates and thus increasing statistical power (Rohlf, 2006).

One of the clearest lacunas in studies that analyse invasive fishes is the comparison of multiple scales and different geographical regions (Table II), although the appropriate basic unit for investigation is probably the drainage basin (Marchetti *et al.*, 2004c; Copp *et al.*, 2005). Patterns of invasion are rarely documented across multiple spatial scales, but research using multi-scale approaches has generated interesting new insights into the invasion process (Pauchard & Shea, 2006). For instance, native and alien species diversity are often positively correlated in large-scale observational studies, but negatively correlated in small-scale experimental studies (Byers & Noonburg, 2003). Similar variables have been used as predictors of invasibility in the studies reviewed here (see e.g. fish richness in Table II), illustrating the potential confounding effect of the study's scale. Similarly, establishment and dispersal might be expected to vary strongly with latitude (disputed by García-Berthou *et al.*, 2005), and the importance of specific life-history traits varying accordingly. For example, the invasion success of rainbow trout *Oncorhynchus mykiss* (Walbaum) depends strongly on the region-specific hydrological regime (Fausch *et al.*, 2001) and other factors, such as the species' susceptibility to whirling disease, caused by a myxozoan parasite *Myxobolus cerebralis* to which native brown trout *Salmo trutta* L. is resistant (Fausch, 2007). Although invasion predictions will have to be taxon- and region-specific (Kolar & Lodge,

2002; Moyle & Marchetti, 2006), the lack of comparison among regions and scales seems clearly a pending task.

SYNTHESIS OF RESULTS

With such a disparity of regions and species, the reduced number of studies, and different variables considered (from three to 27 predictors) and methods used, little comparison among studies might be expected. A closer examination to the predictors identified, however, suggests some consistencies. At the transport and release phases (labelled T/R or R in Table I), two out of three studies (references 6 and 10 in Table I) have identified taxonomic selection, human affiliation and fish size as predictors. These variables, as well as variability in life-history traits also emerge in two of three studies comparing native and introduced species (references 5 and 11 in Table I, with phase labelled 'E/I'). A variable with partial support in many phases is latitudinal range: one of three T/R studies (reference 7), one of three E/I studies (reference 5) and three of seven E studies. Range size is often positively related to body size in fishes, although sometimes through the effect of habitat preference and migration type (Griffiths, 2006), so it will be difficult to distinguish amongst these variables.

The distribution of invasive species among taxonomic families and higher taxa has been shown to be far from random in fishes, plants (Pyšek, 1998; Richardson & Rejmánek, 2004) and birds (Lockwood, 1999; Blackburn & Duncan, 2001). Certain families and taxa clearly have more invasive species. Introduced fishes are often introduced intentionally, with a strong taxonomic bias for game or forage fishes or species with human interest, which often are piscivores and have been introduced elsewhere (Rahel, 2000, 2004; Alcaraz *et al.*, 2005; Clavero & García-Berthou, 2006; Jeschke & Strayer, 2006). For this reason, the only measure of propagule pressure often used is the history of introductions or the number of countries where a species has been introduced (Table II). This taxonomic bias, often for species with presumed different ecological niches, such as piscivores or game fishes, also implies that introduced fishes are often quite different to native species and particularly more diverse in life-history traits (Table I).

Examples of the variability in taxonomy and life-history traits of introduced fishes (in Europe or elsewhere) and the preponderance of human interests or affiliation and taxonomic selection are those ranging from small, live-bearing poeciliid such as mosquitofish, introduced for mosquito control, to piscivorous centrarchids such as largemouth bass *Micropterus salmoides* (Lacepède) or cyprinids such as common carp *Cyprinus carpio* L., introduced for sport or food. These three fish species are also amongst the eight most widely-introduced freshwater fishes (García-Berthou *et al.*, 2005), again reflecting human-mediated taxonomic selection and propagule pressure.

Although establishment is by far the most studied phase, the conclusions are less clear. For example, it has been suggested that successful fish establishment in California seems best predicted with a global model consisting of seven variables, and that predictive models will be habitat- and region-specific and difficult to develop (Marchetti *et al.*, 2004b). In contrast to other phases, for most

studies that examine establishment (with phase labelled E in Table I) the predictors identified are reproductive variables (*e.g.* parental care), diet breadth or environmental tolerances (*e.g.* references 1, 3, 4, 7, 8 *v.* references 6, 10, 12). A reason for these less clear results for establishment might be that introduced fishes have establishment rates that are much higher than many other taxa (García-Berthou *et al.*, 2005; Jeschke & Strayer, 2005), which clearly results from the intentional human-selected nature of the introductions. These higher establishment rates and intentional introductions imply that many species, which are not expected to establish, are not introduced. As a result, the importance of species-specific climate and environment matching will be underestimated with the data.

For the dispersal and integration or impact phases (labels D and I in Table I), the limited number of studies and species further constrain the comparisons. The number of predictors identified for these stages seems lower and less consistent than for the other invasion phases. The traits mediating these phases are poorly understood for other taxa as well (Levine *et al.*, 2003; Dukes & Mooney, 2004; Marchetti *et al.*, 2004c). Although the dispersal of invasive species has been extensively modelled (Fagan *et al.*, 2002; Drake & Lodge, 2004; Ortega-Cejas *et al.*, 2004; Dwyer & Morris, 2006), there is consensus that it is a process more complex than generally acknowledged (Hastings *et al.*, 2005) and little work has been done with fishes (Arim *et al.*, 2006). Again, intentional and accidental introductions of fishes and other invasive species probably differ in their dispersal dynamics, so more data on the dispersal of invasive freshwater fishes are urgently needed before generalizations can be drawn.

As regards the impacts of invasive fishes, so little is known that generalizations surrounding the related species' traits is likely to be premature. Ricciardi & Atkinson (2004) have demonstrated, through a meta-analysis, however, that high-impact invaders (*i.e.* those that displace native species) are more likely to belong to genera not already present in the system. Therefore, taxonomy probably synthesizes a key role, not only in the initial phases (transport and release) but also in the final and most concerning phase (impact). The comparison of invader traits against those of the resident community has been pointed out as potentially very useful for predicting severe impacts (Levine *et al.*, 2003).

RESEARCH NEEDS AND PERSPECTIVES

As reviewed earlier, invasive species represent both urgent research needs, from the conservation point of view, and a unique opportunity to advance ecological understanding. Of the different phases of biological invasions, the introduction phase is amongst the least investigated but perhaps the most important one in both regards (Kolar & Lodge, 2001; Puth & Post, 2005; Jeschke & Strayer, 2006). It is most unfortunate that despite the consensus that propagule pressure is a strong mediator of establishment and dispersal of invasive species (Lockwood *et al.*, 2005) and the potential for confounding with other predictors (Colautti, 2005), there are almost no precise measures of propagule pressure for freshwater fishes (Table II; Copp *et al.*, 2007). For the following

reasons, ecologists should concentrate on obtaining measures of propagule pressure, understanding other phases (introduction and impact), or comparing native and established or invasive species (to understand niche relationships): (1) the establishment phase has been mostly studied, (2) many studies have shown that most introduced fishes have high establishment rates probably because strong human-mediated taxonomic selection and propagule pressure and (3) propagule pressure is poorly known and probably affects the conclusions. Nonetheless, research on the establishment phase should not cease, but investigations of the introduction phase should be given higher priority (Puth & Post, 2005). Data on the transport, sale, release and escapement of freshwater fishes to the wild are needed. Unauthorized and illegal fish introductions (García-Berthou & Moreno-Amich, 2000; Rahel, 2004) should receive more attention both from academic research (*e.g.* frequency, source and types of transports and releases) and from government agencies (mechanisms to reduce it).

Despite the considerable attention that invasive species receive, little data on their dispersal and population dynamics and ecological impacts of invasive (and native) fishes are available, so their effects on native populations, communities and ecosystems are largely unknown (Parker *et al.*, 1999; Simberloff, 2006). Invasions are fundamentally population-level processes, but they are seldom studied as such (Sakai *et al.*, 2001; Peterson *et al.*, 2002). Little is known about the impacts of most invasive species on native species and on ecosystem functioning (Levine *et al.*, 2003; Dukes & Mooney, 2004). More observational and experimental studies on the population ecology and impact of invasive species are urgently needed. The data on ecological effects in Database on Introductions of Aquatic species (DIAS) and FishBase databases are of little use with this regard (Williamson, 1996; García-Berthou *et al.*, 2005), since they are not based on evidence and as a consequence reflect subjective human interests rather than objectively measured ecological effects.

Finally, more integration of approaches is also needed, such as the: analysis of the life-history traits of invasive species along space (*e.g.* latitude) or at multiple scales and exploration of the hypotheses that incorporate characteristics of both the invader and the recipient system (Ricciardi & Atkinson, 2004). The 12 studies reviewed here are good examples of the diversity of possibilities (and difficulties) for studying invasive fishes, but they all deal with fishes in temperate latitudes of the northern hemisphere (Europe and North America). Hopefully, this review will stimulate and help initiate similar studies in other regions and latitudes in order to promote the conservation of the enormous diversity of freshwater ecosystems.

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