

# Profiling invasive fish species: the importance of phylogeny and human use

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## ABSTRACT

Understanding the ecological differences between native and invasive species is of considerable scientific and practical interest. We examined such differences between native and invasive inland fish species from the Iberian Peninsula in order to analyse the importance of phylogenetic correction and variability (in addition to central tendency). We collected 26 quantitative and qualitative variables on the ecology, life-history traits and human use of the 69 inland fish species of the Iberian Peninsula, including native, invasive and migratory species. The taxonomic distribution of invasive fish species deviated significantly from world freshwater richness and in contrast to native species, invasive fish belongs to only five taxonomic orders but to a wide spectrum of families not native to the Iberian Peninsula. Because the life-history traits were highly dependent on taxonomy, the results, with or without applying phylogenetic methods, differed and after accounting for phylogeny, invasive species displayed higher and wider latitude in general and a different reproductive season mainly among salmonids and cyprinids. Human use was also significantly different between native and invasive fish species and produced more variability in life-history traits of invasive species and uneven taxonomic distribution because of the high diversity of species introduced. We show that accounting for taxonomy and studying variability in addition to central tendency is important in the comparison of life-history traits between native and invasive species.

## Keywords

Biological invasions, Iberian Peninsula, independent contrasts, introduced species, Levene test, life-history traits, variance.

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## INTRODUCTION

Biotic homogenization through the introduction of invasive species and extinction of native species is now recognized as one of the main threats to biodiversity and ecosystem function (Mack *et al.*, 2000; Rahel, 2002; Clavero & García-Berthou, 2005). Predicting future invader species and vulnerable ecosystems is of immense scientific and practical interest (Rejmánek & Richardson, 1996; Ricciardi & Rasmussen, 1998; Mack *et al.*, 2000). Among several approaches (Mack, 1996; Rejmánek, 2000), many studies have attempted to identify the distinctive biological traits of invasive species, although the results have been often inconclusive (Pyšek, 1998; Goodwin *et al.*, 1999; Mack *et al.*, 2000). In general, invasive species have been suggested to be of wide geographical range, abundant, generalists, tolerant to abiotic factors and human commensals (Williamson, 1996; Ricciardi & Rasmussen, 1998; Lockwood, 1999).

One of the most common methods of identifying biological traits of invaders is by comparing two sets of species in a given region, e.g. successful vs. unsuccessful introductions (Forsyth

*et al.*, 2004; Marchetti *et al.*, 2004), native species vs. established introductions (Williamson & Fitter, 1996; Vila-Gispert *et al.*, 2005) or invasive vs. noninvasive introduced species (Kolar & Lodge, 2001). Such comparisons provide different information because different species characteristics may determine success in different invasion transitions (transport, establishment and invasion) (Kolar & Lodge, 2001). Comparing native and established invasives is the information most widely available (because unsuccessful introductions and invasive potential are poorly known) and may help understand the overall success of invasive over native species (niche overlap, reproductive ability), whereas other types of comparisons may provide information on specific invasion transitions. Except in a few recent studies of introduced mammals and birds (Duncan *et al.*, 2001; Cassey *et al.*, 2004; Forsyth *et al.*, 2004), all these comparisons have been usually performed without controlling for phylogenetic effects, particularly for fish (Fisher & Owens, 2004). Taxonomy has actually hardly been tested as a predictor of invasiveness (Lockwood, 1999). However, it is well appreciated in comparative studies that treating closely related species as independent data may violate

the independence assumption of most statistical methods (Harvey & Pagel, 1991; Garland *et al.*, 1999). The distribution of invasive species among taxonomic families and higher taxa has been shown to be far from random in plants (Pyšek, 1998; Richardson & Rejmánek, 2004) and birds (Lockwood, 1999; Blackburn & Duncan, 2001), and certain families and taxa have more invasive species. In a review of life-history data for 301 fish species in general (Vila-Gispert *et al.*, 2002), taxonomic order was found more important than latitude, habitat or geographical region in determining life-history traits. Therefore, the potential of confounding taxonomy with biological attributes as determinants of invasiveness is great.

Freshwater ecosystems are especially prone to biological invasions, in part because of habitat alteration and degradation (Moyle & Light, 1996a; Rahel, 2002). The impacts of invasive freshwater fish are variable and poorly understood but include some of the most dramatic cases (Drake *et al.*, 1989; Moyle & Light, 1996a) and the Iberian Peninsula is no exception to this (García-Berthou & Moreno-Amich, 2000; Elvira & Almodóvar, 2001). However, there are few studies that try to assess the distinctive features of successful invasive freshwater fish (Kolar & Lodge, 2001; Marchetti *et al.*, 2004; Vila-Gispert *et al.*, 2005). The objectives of this paper are: (1) to test whether there are ecological or human use differences between native and invasive inland fish species from the Iberian Peninsula, (2) to assess whether phylogenetic correction is necessary to analyse such data and (3) to test whether there are differences in variability of characters in addition to central tendency.

## METHODS

### Data set

We assembled data for the 69 inland fish species of the Iberian Peninsula (Doadrio, 2002), including native, invasive and migratory inland species but excluding fish of marine origin (see pp. 97–98 of Doadrio (2002) for a full list of species). Invasive species are considered in this paper as non-native species that have established self-sustaining wild populations (stages III to V of Colautti & MacIsaac, 2004). Note, however, that a few of the fish species considered, both native (e.g. *Acipenser sturio*) and invasive (e.g. *Oncorhynchus kisutch*), have small populations in the Iberian Peninsula with uncertain status. Moreover, a few fish species introduced more recently have not been considered, whereas the introduced status and taxonomy of a few species (e.g. *Gobio gobio*) is being currently revised.

The reference sources for the compilation of the life-history, ecological and human use variables were Maitland (2000), Doadrio (2002), FishBase (Froese & Pauly, 2003) and Vila-Gispert *et al.* (2005). We considered the following 14 qualitative variables: taxonomic order and family; use in aquaculture (yes/no); use in aquarium (yes/no); use as bait (yes/no); use as game fish (yes, occasionally, or no); fisheries exploitation (yes/no); feeding type classified as invertebrate, omnivore, piscivore, zooplanktivore, or other (including parasites and lampreys); reproductive guild (phytophils, phytolithophils, lithophils, inter-

nal or marine) from Mann (1996); habitat (lentic, lotic or generalist); salinity tolerance (yes/no); marine (yes/no); microhabitat (benthic, neustonic, pelagic or generalist) and climatic region (polar, temperate, subtropical or tropical). We also considered the following 12 quantitative variables: maximum reported age for the species (years), mean and maximum fecundity (number of eggs), age at maturity (years), mean and maximum observed total length (to the nearest cm), minimum record and range of habitat temperature (°C), maximum record and range of latitude (°N), midpoint of the reproductive season (month) and reproductive season span (number of months).

### Statistical analyses

To test for differences in the frequency of qualitative variables between native and invasive species we used *G*-tests of independence (Sokal & Rohlf, 1995). A multiple binary logistic regression model using a stepwise selection procedure (based on the likelihood ratio) was also used to identify qualitative variables that showed the most important differences between invasive and native species (Tabachnick & Fidell, 2001). Logistic regression is a generalized linear model with binomial distribution and a logit link function, suitable for categorical dependent variables (Quinn & Keough, 2002).

To test for taxonomic selection, we also compared the number of Iberian invasive species with the world number of freshwater fish species by taxonomic order (Nelson, 1994) using the binomial distribution as detailed in Lockwood (1999). For this particular test, esociform fish species (only introduced *Esox lucius* in the Iberian Peninsula) were distinguished from Salmoniformes (cf. Doadrio, 2002) to match Nelson's usage.

Quantitative variables were analysed with two-sample *t*-tests (Sokal & Rohlf, 1995) and Levene tests. The former compares the means of two groups, whereas Levene tests compare the variances of two or more groups and are more robust than other homogeneity-of-variance tests (Quinn & Keough, 2002). For midpoints of reproductive season and reproductive season span, the guppy (*Poecilia reticulata*) data were excluded from the analyses because of its distribution limited in the Iberian Peninsula to a single, peculiar locality.

When many statistical tests are performed on some data, there is an increased risk of type I errors (wrongly rejecting null hypotheses). To overcome this, we used the procedure of Benjamini and Hochberg (1995), as implemented in the *R* package (R Development Core Team, 2003), for both quantitative and qualitative variables. This procedure controls the false discovery rate, i.e. the expected proportion of false discoveries amongst the rejected hypotheses, instead of the probability of a single type I error in the familywise error rate procedures (e.g. the usual Bonferroni or Holm corrections). The Benjamini and Hochberg (1995) procedure has more statistical power and robustness than familywise error rate procedures among other advantages (García, 2004).

We used discriminant function analysis (DFA) to determine which variables discriminate most between native and invasive species and try to predict group membership from the multivariate set of

quantitative variables. DFA creates functions that are linear combinations of the independent variables so that they separate the groups as much as possible. The regular and stepwise procedures of DFA (Tabachnick & Fidell, 2001) were applied. To explore patterns of association among quantitative variables and to ordinate species, the principal component analysis (PCA) was applied to the correlation matrix. Kaiser-Meyer-Olkin's (KMO) measure of sampling adequacy was used to assess the usefulness of a PCA. KMO ranges from 0 to 1 and should be well above 0.5 if variables are interdependent and a PCA is useful (Tabachnick & Fidell, 2001).

Because closely related species may share a similar suite of traits through common ancestry, treating species as independent data points in a comparative study may confound differences between groups (e.g. invasive vs. native) with phylogeny (e.g. differences between orders) (Harvey & Pagel, 1991; Duncan *et al.*, 1999; Garland *et al.*, 1999). As a phylogenetic comparative method, we applied Felsenstein's (1985) method of independent contrasts, as implemented in the COMPARE 4.4 package (Martins, 2003). The independent contrast method calculates the standardized difference between the values of the traits of sister taxa in a phylogeny. A 'contrast' quantifies the amount of evolutionary change that has occurred in a trait after the divergence of sister taxa from a common ancestor. Contrasts are calculated at all levels of a phylogeny by using reconstructions of ancestral states for internal nodes (Williams & Kay, 2001). Pearson's linear correlations are then used to test for correlations between the contrasts of the quantitative variables and the contrasts for invasive status.

The construction of the phylogenetic tree was based on published phylogenies (Parenti, 1981; Kendall, 1988; Smith & Stearley, 1989; Doadrio & Perdices, 1997; Helfman & Collette, 1997; Doadrio, 2002). As we had several missing values for some variables, phylogenies were adapted for each quantitative variable and introduced in COMPARE 4.4.

To further understand the effect of phylogeny on selected quantitative variables, we also estimated the variance components explained by different taxonomic levels (orders, families, genera, and species) [see Jordano (1995) for a similar application]. Variance components analysis (Searle *et al.*, 1992) was performed as a nested design (VARCOMP procedure in SPSS) with all factors treated as random-effects factors except the main one (taxonomic order in our case). All statistical analyses in this paper were performed with SPSS for Windows 11.5 (except when R or COMPARE are mentioned) with the default options (except when other are mentioned).

## RESULTS

### Univariate analyses

After correcting for multiple testing, native and invasive species significantly differed in the proportions of eight of the 14 qualitative variables: order, family, use in aquaculture, aquaria, as game fish or fisheries exploitation, reproductive guild and habitat (Table 1).

Of the 69 Iberian inland species, the 45 native fish belong to 13 different orders, whereas the 24 invasive species only belong to

**Table 1** Independence tests of qualitative variables of the inland fish in the Iberian Peninsula with species status (invasive or native). *P* values have been adjusted by the procedure of Benjamini & Hochberg (1995)

Variable	G	d.f.	P
Order	32.71	13	0.009
Family	45.63	23	0.011
Aquaculture use	20.49	1	0.002
Aquarium use	27.15	1	0.002
Bait use	1.70	1	0.710
Game fish use	5.30	1	0.037
Fisheries exploitation	6.28	1	0.024
Feeding type	5.93	4	0.250
Reproductive guild	15.60	4	0.011
Habitat	9.35	2	0.021
Salinity tolerance	4.49	1	0.053
Marine	0.29	1	0.690
Microhabitat	8.37	3	0.055
Climate	1.69	3	0.690

five different orders. One of these orders is only represented by invasive species (three siluriform species). Moreover, the proportion of world species that have been introduced depended on taxonomic order ( $G = 41.1$ , d.f. = 33, Monte Carlo  $P < 0.0005$ ). Salmoniform fish significantly showed positive selection because the proportion of species that have been introduced (four of about 45) is much higher than for the rest of orders (Table 2). Characiform fish species are underrepresented and esociforms are overrepresented among invasives but this pattern was not significant after correcting for multiple comparisons.

The 45 native species belong to 16 families, whereas invasive species to 11 different families. Eight of these families (Centrarchidae, Cichlidae, Esocidae, Fundulidae, Ictaluridae, Percidae, Poeciliidae and Siluridae) are only represented by invasive species. The Cyprinidae is the most important family, with 24 native species (20 of the 25 Iberian endemic species are Cyprinidae) but only has seven invasive species.

With regard to the human use of these species, we found that invasive fish species are often used in aquaculture (67% of the invasive species), aquaria (88%), as game fish (67%) or commercially exploited (52%) in contrast to native species (respective percentages 13%, 24%, 38% and 21% of native species).

Referred to species biology, differences were found in the reproductive guild: 46% of the invasive species are phytofiles (for only 14% of the native species), whereas native species are mainly lithophils (61% vs. 29% of the invasive species). Internal reproduction is only present in invasive poeciliids (*P. reticulata* and *Gambusia holbrooki*), and only two native species reproduce in deep sea (*Anguilla anguilla* and *Platichthys flesus*). For the habitat, 79% of invasive vs. 47% of native species are lentic; 40% of native vs. 8% of invasive species are generalists (present in both lentic and lotic waters). We did not find significant differences in feeding type, salinity tolerance, marine habits, microhabitat and climatic region between invasive and native species.

**Table 2** Number of native and invasive inland fish species in the Iberian Peninsula by taxonomic order compared to the total number of freshwater fish species (Nelson, 1994). *R* values are the binomial probabilities to the test for taxonomic selectivity of invasive species, comparing the Iberian invasives with the world pool of freshwater species (Lockwood, 1999). *P* values are the *R* values adjusted for multiple comparisons by the procedure of Benjamini & Hochberg (1995)

Order	Number of freshwater species	Number of Iberian natives	Number of Iberian invasives	<i>R</i>	<i>P</i>
Petromyzontiformes	32	3	0	0.926	0.998
Carcharhiniformes	1	0	0	0.998	0.998
Rajiformes	24	0	0	0.944	0.998
Ceratodontiformes	1	0	0	0.998	0.998
Lepidosireniformes	5	0	0	0.988	0.998
Polypteriformes	10	0	0	0.976	0.998
Acipenseriformes	14	1	0	0.967	0.998
Semionotiformes	6	0	0	0.986	0.998
Amiiformes	1	0	0	0.998	0.998
Osteoglossiformes	217	0	0	0.593	0.998
Anguilliformes	6	1	0	0.986	0.998
Clupeiformes	72	2	0	0.841	0.998
Gonorynchiformes	28	0	0	0.935	0.998
Cypriniformes	2662	28	7	0.145	0.822
Characiformes	1343	0	0	0.039	0.444
Siluriformes	2280	0	3	0.114	0.775
Gymnotiformes	62	0	0	0.861	0.998
Esociformes	10	0	1	0.024	0.401
Osmeriformes	42	0	0	0.904	0.998
Salmoniformes	45	2	4	4.54 10 <sup>-6</sup>	0.0002
Percopsiformes	9	0	0	0.979	0.998
Ophidiiformes	5	0	0	0.988	0.998
Gadiformes	1	0	0	0.998	0.998
Batrachoidiformes	5	0	0	0.988	0.998
Mugiliformes	1	0	0	0.998	0.998
Atheriniformes	146	1	0	0.703	0.998
Beloniformes	51	0	0	0.884	0.998
Cyprinodontiformes	794	2	4	0.082	0.700
Gasterosteiformes	19	2	0	0.955	0.998
Synbranchiformes	84	0	0	0.817	0.998
Scorpaeniformes	52	1	0	0.882	0.998
Perciformes	1922	1	5	0.173	0.840
Pleuronectiformes	4	1	0	0.990	0.998
Tetraodontiformes	12	0	0	0.971	0.998

As an indicative summary, a logistic regression analysis (stepwise procedure,  $P < 0.05$ ) of all the qualitative variables selected aquarium ( $P = 0.003$ ) and aquaculture ( $P < 0.0005$ ) uses and reproductive guild ( $P = 0.001$ ) as the most important variables distinguishing invasive and native species (Nagelkerke  $R^2 = 0.78$ ).

Analyses of quantitative variables revealed that invasive and native species showed different variances in two of the variables analysed: reproductive season span and latitude range (Table 3). In contrast, no variable showed significant differences in central tendency between native and invasive species ( $t$ -test without correcting for phylogenetic effects).

The central tendency of reproductive season span is similar for the two groups but invasive species display more variance than native ones (Fig. 1). Most species have a reproductive season of

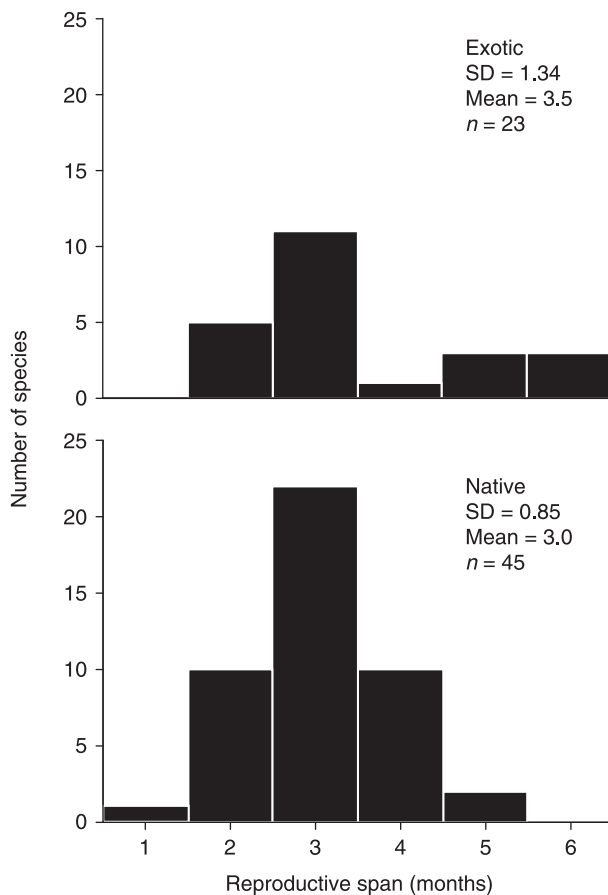
2 to 3 months but several invasive species (poeciliids and some salmonids) have much longer seasons ( $\geq 5$  months). The variability and distribution of latitudinal range is very different between native and invasive species. Native species are significantly more variable than invasive species and display a bimodal distribution with two groups, one with European species of wide distribution and the other with Iberian endemic species (Fig. 2).

### Multivariate analyses

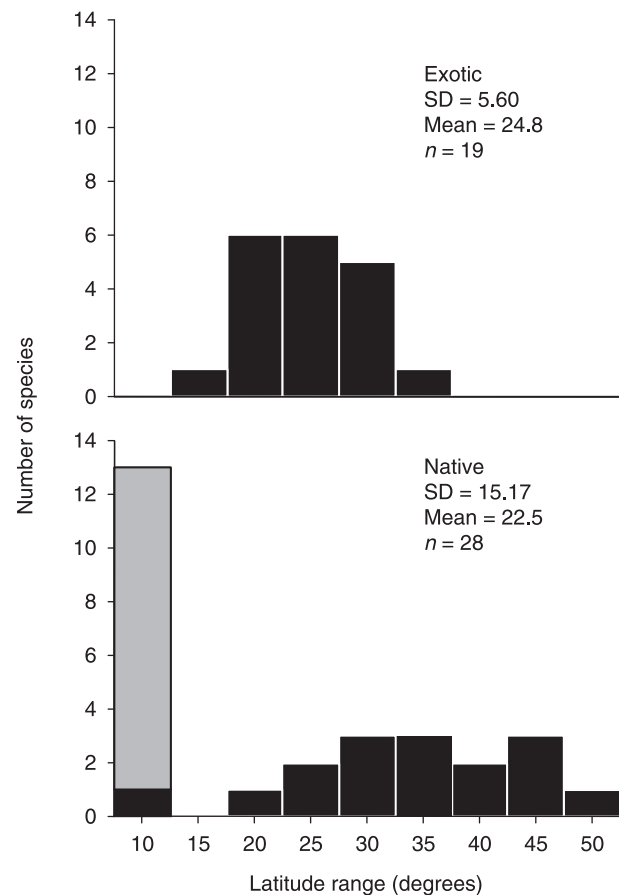
Although a stepwise DFA suggested that age at maturity and maximum age significantly discriminated between native and invasive species (Wilks's  $\lambda = 0.58$ ;  $\chi^2 = 13.6$ ;  $P = 0.001$ ), it only predicted correctly the origin status for 44.9% (cross-validated)

**Table 3** Differences in the quantitative variables between invasive and native species of freshwater fish in the Iberian Peninsula. Levene tests compare the variance of invasive and native species, whereas other tests compare the central tendency. The *t*-tests correspond to the separate variance formula (not assuming homoscedasticity) of the two independent sample test. *P* values have been adjusted by the procedure of Benjamini & Hochberg (1995). A positive correlation in the independent contrasts indicates a larger mean for invasive species (and vice versa)

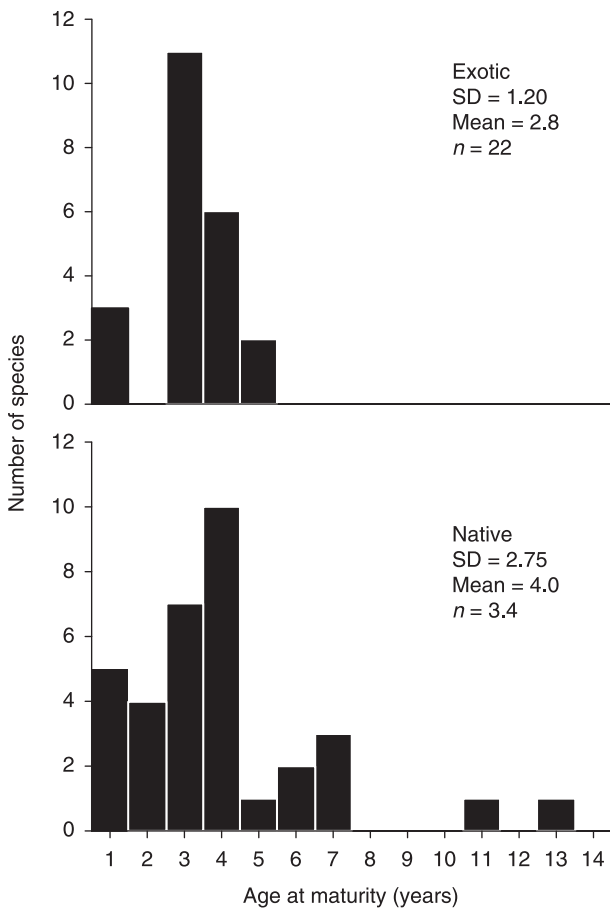
Variable	Levene test		<i>t</i> -test			Independent contrasts		
	<i>F</i>	<i>P</i>	<i>t</i>	d.f.	<i>P</i>	<i>r</i>	<i>N</i>	<i>P</i>
Maximum reported age	0.99	0.48	0.19	47.0	0.85	-0.011	50	0.94
Mean total length	0.29	0.71	0.95	46.5	0.35	0.069	62	0.59
Max. observed total length	3.83	0.15	-1.41	30.8	0.17	0.078	68	0.53
Age at maturity	5.01	0.12	-1.66	48.7	0.10	-0.123	55	0.37
Mean fecundity	2.69	0.26	-1.08	33.7	0.29	-0.038	54	0.78
Maximum fecundity	2.42	0.26	-0.97	38.7	0.34	-0.025	55	0.86
Midpoint of reproductive season	1.61	0.36	-0.47	36.8	0.74	-0.272	67	0.026
Reproductive season span	9.13	0.024	1.41	31.3	0.17	0.119	67	0.34
Mean habitat temperature	0.004	0.98	1.89	33.5	0.07	0.193	40	0.32
Temperature range	0.42	0.69	1.70	38.8	0.10	0.042	40	0.80
Mean latitude	0.001	0.98	1.28	36.8	0.21	0.318	46	0.031
Latitude range	29.88	0.003	0.75	36.7	0.46	0.313	46	0.034
PCA 1 score	0.37	0.85	1.26	45.4	0.22	0.130	65	0.30
PCA 2 score	5.30	0.025	1.44	30.7	0.16	-0.043	65	0.73



**Figure 1** Length of the reproductive season span for the native and invasive inland fish species in the Iberian Peninsula. SD = standard deviation, *n* = number of fish with data.



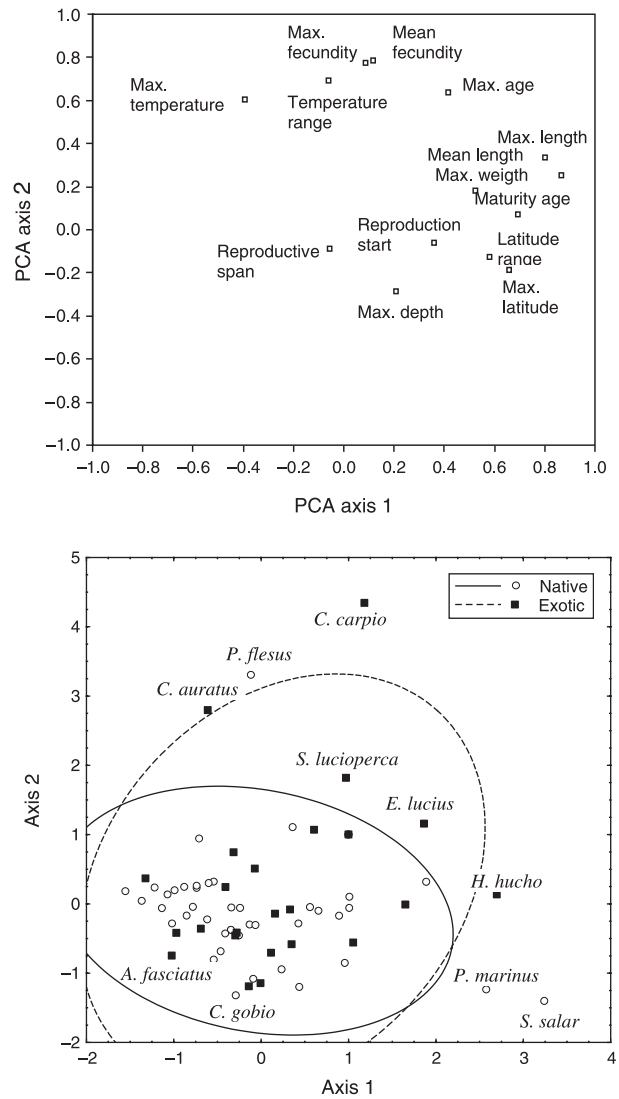
**Figure 2** Latitude range for the native and invasive inland fish species in the Iberian Peninsula. The grey colour indicates species endemic to the Iberian Peninsula.



**Figure 3** Age at maturity for the native and invasive inland fish species in the Iberian Peninsula.

of the species, and is therefore useless. A similar result was obtained with regular DFA. The seven species with highest age at maturity are all native but there is no significant difference in central tendency (Fig. 3).

Most of the variables were correlated and the KMO's measure of sampling adequacy (0.61) indicated the usefulness of a PCA, and the two first axes explained 24.6% and 20.2% of the variation, respectively. As also seen with the factor loadings (Fig. 4), the highest correlations were found between length, age at maturity, maximum latitude, and latitude range which were all positively correlated. The first PCA axis identified a dominant gradient of ecological and life-history traits that contrasts species with large size, late maturation, and from high and more diverse latitudes (such as *Salmo salar*, *Petromyzon marinus* and *Hucho hucho*) with small species, early maturation, and from low and narrower range of latitudes (such as *G. holbrooki*, *Aphanius iberus* and *Chondrostoma lemmingii*) (Fig. 4). The second axis contrasts species with higher fecundities, higher longevities, and from higher and wider ranges of temperature (e.g. *Cyprinus carpio*, *P. flesus* and *Carassius auratus*) with species with the opposite suite of traits (e.g. *Cottus gobio*, *Phoxinus phoxinus* and *Lampetra planeri*). There are no significant differences of mean PCA scores with species origin but invasive species are more variable in the PCA 2 scores than native ones (Fig. 4, Table 3).



**Figure 4** Principal components analysis of the 14 quantitative variables for native and invasive inland fish species of Iberian Peninsula. Top, factor loadings of the variables; bottom, species scores on the first two principal component axes (with 95% confidence ellipses). Symbols and ellipses identify the two groups (native and invasive).

### The effect of phylogeny

Once the phylogenetic effect was eliminated, three variables (midpoint of reproductive season, mean latitude and latitude range) that were previously not significant (*t*-tests) now showed significant differences in central tendency between native and invasive species (independent contrasts, Table 3). Thus, although overall differences in latitude and reproductive season were small (Figs 2, 5 & 6), there were significant differences after accounting for phylogeny (i.e. within the same order or family) because the differences within families were larger and sometimes opposite. Among the families with enough information (i.e. with larger number of species), invasive salmonids reproduced on average 1.6 months before than the two native species, whereas the invasive



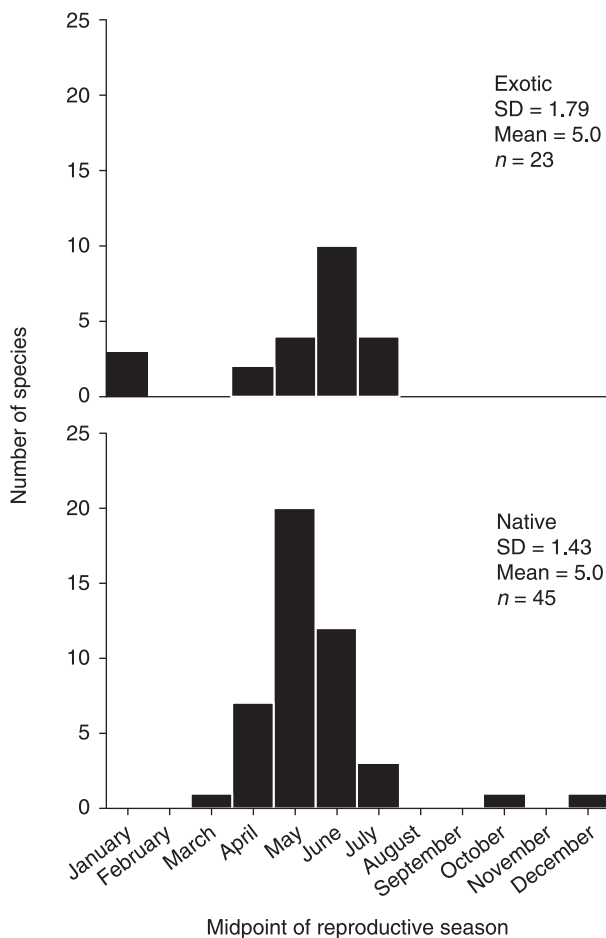


Figure 5 Midpoint of the reproductive season span for the native and invasive inland fish species in the Iberian Peninsula.

cyprinids reproduced 0.8 month later than native cyprinids. Many of the invasive cyprinids (e.g. *Rutilus rutilus*, *Scardinius erythrophthalmus*, *Alburnus alburnus*) are central European species with wide distributions in contrast to native species, many of which are endemic to the Iberian Peninsula (so with smaller latitudinal range).

Partitioning of trait variation among categories in the taxonomic hierarchy (Fig. 7) suggests high similarity in latitude range, age at maturity, length and fecundity among close phylogenetic relatives (i.e. among species of a certain genus or family). On average, phylogenetic effects at the ordinal and familial levels explain about 80% of the total variation in age at maturity, length and fecundity. This outcome suggests that age at maturity, length and fecundity are largely intrinsic and relatively stable characters of higher taxonomic levels (order and family). For instance, salmoniforms are usually large-sized with late maturation and high fecundities, whereas cyprinodontiforms display the opposite suite of traits. This pattern contrasts with the greater generic and specific effects exhibited by midpoint of reproductive season and its span and temperature and latitude range (Fig. 7). These characters are less influenced by phylogeny, and consequently, more variable between closely related species. This is in agreement with the above observation that invasive fish species spawn

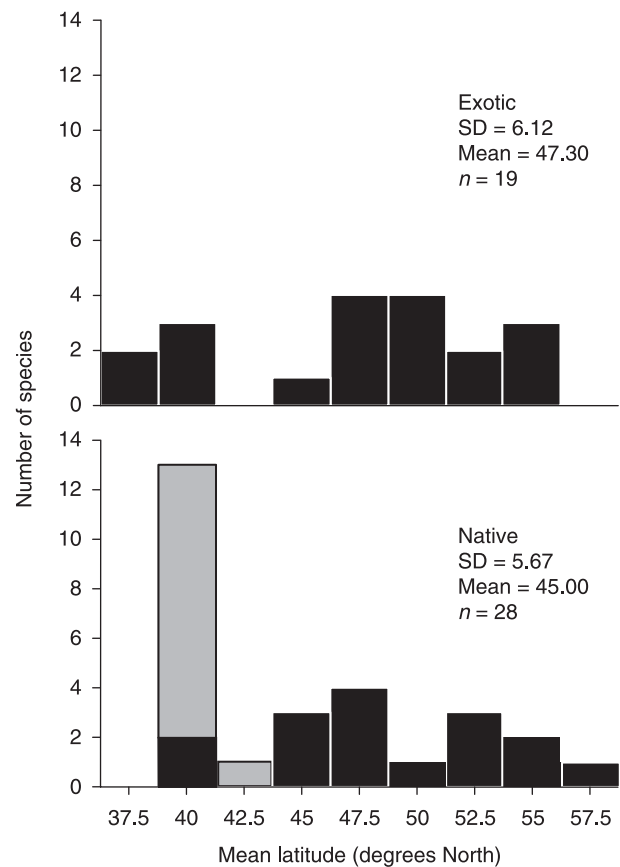


Figure 6 Mean latitude for the native and invasive inland fish species in the Iberian Peninsula. The grey colour indicates the Iberian endemic species.

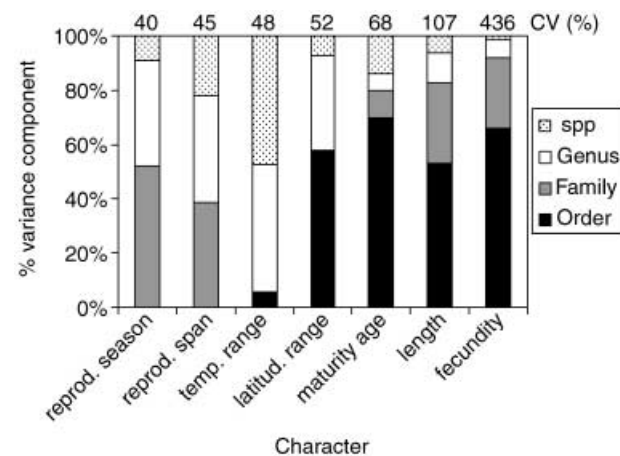


Figure 7 Variance components of different taxonomic levels (order to species) for selected quantitative traits of Iberian inland fish species. Figures at the top are the coefficients of variation (CV = 100 SD/mean).

before and come from higher and wider ranges of latitudes than native ones.

Age at maturity, length and fecundity are more variable [coefficient of variation (CV), Fig. 7] and differences are mainly related to orders, whereas midpoint of reproductive season,

reproductive season span, and temperature and latitude range are less variable (Fig. 7) and differences are mainly attributable to genus and species. CV was significantly related to the percentage of variation explained at the ordinal level (Spearman's  $r_s = 0.81$ ,  $N = 7$ ,  $P = 0.027$ ), so characters more variable have more phylogenetic inertia (Blomberg & Garland, 2002).

## DISCUSSION

### Differences between native and invasive fish species: the importance of phylogeny

The number of species by taxonomic order and family significantly differed between native and invasive species. In contrast to native fish, invasive species belong to only five taxonomic orders (Cypriniformes, Salmoniformes, Perciformes, Cyprinodontiformes and Siluriformes) but to a wide spectrum of families not native to the Iberian Peninsula (Centrarchidae, Cichlidae, Esocidae, Fundulidae, Ictaluridae, Percidae, Poeciliidae and Siluridae). We also found that salmoniform fish species are significantly over-represented among invasives in relation to their world richness. The taxonomic distribution of invasive fish species is thus not random, as has been previously found for plants (Pyšek, 1998; Richardson & Rejmánek, 2004) and birds (Lockwood, 1999; Blackburn & Duncan, 2001). As for plants and birds, this seems clearly related to the purposeful introduction of species of human interest. In the Iberian Peninsula, invasive fish species were mainly introduced as game fish or for use in aquaculture or in aquarium. As also pointed out by Lockwood *et al.* (2001), there is a tendency for invaders to come from taxa that are not represented in the native fauna. Invasive species may be more successful if they are ecologically distinct from members of the community that they are invading (Lockwood *et al.*, 1993; Moyle & Light, 1996b; Williamson, 1996) because they may be able to exploit a resource untapped by native species, avoiding competition with native species or may be free of predators or parasites (Lockwood *et al.*, 2001), although biotic resistance has been suggested to be less important than abiotic factors in determining the success of invasive fish in California streams and estuaries (Moyle & Light, 1996a).

If fish introduced to the Iberian Peninsula has a taxonomic bias, this may affect the comparison of life-history traits between native and invasive species. Without correcting for phylogeny, there were not significant mean differences in any trait between native and invasive species but after controlling for phylogeny, midpoint of reproductive season, mean latitude and latitude range became significantly different between native and invasive species. In general, trait differences vanish after accounting for phylogenetic effects, indicating that the differences between groups were caused at least in part by phylogeny (Jordano, 1995). But in some cases, nonsignificant differences may turn significant (Villar *et al.*, 1998; Duncan *et al.*, 2001) as was also observed in our study, indicating that phylogenetic correction is thus necessary to partial out strong taxonomic effects and allow more powerful comparisons between native and invasive species within orders or families. Because many fish life-history traits are highly

dependent on phylogeny (Vila-Gispert *et al.*, 2002), phylogenetic methods may detect subtle differences within families. Since most Iberian fish species are cyprinids (51%) or salmonids (10%) this seem particularly worthy.

### Predicting the traits of invasive fish species: variable human interests

Taxonomy and human use are the main factors differentiating native and invasive fish species in the Iberian Peninsula. It is more difficult to make generalizations about which life-history traits are characteristic of invasive fish species. We found that several life-history traits were not significantly different between native and invasive fish species on average but showed differences in variability (Table 3). Reproductive season span of invasive species is more variable, from species with protracted spawning seasons (e.g. *G. holbrooki*) to those with short spawning seasons (e.g. *R. rutilus*). In contrast, native fish fauna is more variable in latitude range as a result of a mixture of many Iberian endemisms (with small ranges) and some species with wide distributions. PCA also showed that invasive species are more variable in a suite of attributes such as fecundity, longevity, and temperature tolerance. The higher variability of life-history traits among invasive species should be expected from the contrasting human uses of these species that range from small species mainly selected for aquarium purposes such as *P. reticulata* or *G. holbrooki* to large species typically used in aquaculture such as salmoniforms. Human interests in fish introductions are diverse and thus obscure life-history trait characterization of invasive fish species.

After controlling for phylogeny, midpoint of reproductive season, mean latitude and latitude range significantly differed between native and invasive species. Invasive fish species came from higher and wider latitudes. Many researchers have previously noted the importance of latitudinal range to invasiveness (Scott & Panetta, 1993; Ricciardi & Rasmussen, 1998; Duncan *et al.*, 1999; Goodwin *et al.*, 1999; Duncan *et al.*, 2001). Invasive species with a wide distribution are likely to succeed in a new environment because of their wide environmental tolerances (Goodwin *et al.*, 1999; Marchetti *et al.*, 2004). Wide geographical range could indicate flexible or generalist species that have a high chance of success because they are likely to encounter conditions suitable for establishment (Williamson, 1996).

The difference in reproductive season was only significant after accounting for phylogeny and was depended on family. Introduced cyprinids spawned later than native cyprinids, whereas the opposite was the case for salmonids, of which, the two native species spawn in autumn, whereas the invasive spawn rather in winter or spring. The species-specific timing of salmonid recruitment and its relationship to the local hydrologic regime has been recently suggested as a key factor in explaining the invasive success of salmonids (Fausch *et al.*, 2001).

In a previous study, we found that fecundity and age at maturity significantly distinguished native and invasive fish species from Catalan streams (Vila-Gispert *et al.*, 2005), in contrast to the present results that did not find such differences even prior to phylogenetic correction. We believe that these contrasting results



are caused by the wider geographical scale of the present study, which implies a larger set of different species.

In conclusion, the identification of life history and ecological traits differential of invasive species features will benefit from the incorporation of phylogenetic methods and an appraisal of variability in addition to central tendency of characters. Studies at different geographical scales may also yield different results and an understanding of the underlying mechanisms.

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