Heads you win, tails you lose: Life-history traits predict invasion and extinction risk of the world's freshwater fishes

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Abstract
1. Freshwater fishes have the distinction of being both a highly imperilled taxonomic group as well as one that has produced many invasive species with widespread ecological impacts. Faced with the difficult task of identifying those species with the greatest need for management action, ecologists have turned to using predictive suites of ecological and life-history traits to provide reasonable estimates of fish invasion and extinction risk. Whether traits associated with invasiveness are the inverse of those associated with imperillment, known as the ‘two-sides-of-the-same-coin’ hypothesis, remains unclear.

2. A global trait analysis (including maximum total body size, longevity, size at maturation, age at maturation, fecundity and egg size) for 6293 freshwater fishes was conducted to examine the trait correlates of species proneness to invasion or extinction. A meta-analytical procedure was deployed using univariate and multivariate trait analyses that accounted for the effects of shared phylogeny.

3. Mean trait differences (measured as Hedges’ d effect size) were found between invasive and threatened species when compared with native species, thus supporting the two-sides-of-the-same-coin hypothesis for freshwater fish. Invasive species were characterized by larger body size, greater longevity, delayed maturation and higher fecundity than threatened species. Furthermore, invasive species were found to display greater trait variability compared with threatened species, suggesting that different traits may be selected at different stages of the invasion process (from pathway entrainment to establishment) whereas more specific trait combinations may predispose species to higher extinction risk.

4. The present study demonstrated a strong trait basis to global-scale invasion risk and extinction vulnerability for freshwater fishes. Given that both time and resources are too limited for detailed species-by-species assessments, the results suggest that trait correlates provide a reasonable estimate of invasion and extinction risk that can inform more targeted and proactive conservation strategies.

KEYWORDS
alien species, conservation planning, endangered species, functional diversity, homogenization, species extinction

1 | INTRODUCTION

The dual processes of species invasion and extinction continue to operate at unprecedented rates, contributing to the massive reshuffling of biotas and a global biodiversity crisis (Almeida & Grossman, 2014; Baiser, Olden, Record, Lockwood, & McKinney, 2012; Ceballos et al., 2015; Matsuzaki et al., 2011). Developing effective risk assessment protocols aimed at identifying species that are likely to become successful invaders or threatened in the near future is an urgent need (Howeth et al., 2016; Olden, Poff, & Bestgen, 2006, 2008). Mounting evidence suggests that animal and plant responses to extrinsic factors, such as habitat modification, over-exploitation and climate change, can vary depending on their intrinsic vulnerability, as mediated by a suite of life history, physiological and...
that traits influencing invasion success were not opposite to those associated with extinction vulnerability. Resolution regarding the generality of the two-sides-of-the-same-coin hypothesis, especially at broad spatial scales, thus remains unclear.

The present study provided a global investigation of the association between life-history traits and the risk of species invasion or extinction for freshwater fishes. Using a meta-analytical approach and the most comprehensive global trait database for freshwater fish species to date, the two-sides-of-the-same-coin hypothesis was tested by comparing the direction and magnitude of trait differences between invasive and threatened species compared with congeneric native species. The present study is the first to explore the role of multiple traits on both animal invasiveness and imperilment for a major taxonomic group at the global scale.

2 MATERIALS AND METHODS

2.1 Global trait database for freshwater fishes

Species trait data for 6293 freshwater fishes, representing approximately 40% of the global freshwater fish species pool (15 750 species; Closs, Krkosek, & Olden, 2016), were assembled based on a comprehensive review of the literature and online databases. The inclusion of species was determined by data availability based on six life-history traits previously shown to be associated with fish invasion and extinction (Angermeier, 1995; Duncan & Lockwood, 2001; Marr et al., 2013; Olden et al., 2006; Reynolds et al., 2005). Traits included maximum total body size (mm), longevity (defined as the maximum potential life span in years), total body size at maturation (mm), age at maturation (years), fecundity (defined as the total number of eggs or offspring per breeding season), and egg size (defined as the mean diameter of mature (fully yolked) ovarian oocytes in mm) (Table 1). Trait assignments were based on a multi-tiered data collection procedure. First, trait data were collected from species accounts in the comprehensive texts of the regional fish faunas (Kottelat & Freyhof, 2007; Liu & Qin, 1987; Miller, Norris, & Miller, 2005; Mims, Olden, Shattuck, & Poff, 2010; Olden, Kennard, & Pusey, 2008; Skelton, 2001; Xie, 2007; full references available upon request). Second, species descriptions from the primary literature, government reports, university reports, and graduate theses were used, as discovered by bibliography searches on Thompson ISI Web of Science and the Google Scholar search engine. Searches were conducted for each species using its scientific name as a search query, and all results up to the 50th entry were examined. For species that produced considerably fewer results (<10 records), a new search was conducted using the appropriate

<table>
<thead>
<tr>
<th>Trait</th>
<th>Invasive</th>
<th>Native</th>
<th>Threatened</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maximum body size</td>
<td>388 (100%)</td>
<td>4695 (100%)</td>
<td>1210 (100%)</td>
<td>6293</td>
</tr>
<tr>
<td>Longevity</td>
<td>222 (57%)</td>
<td>1105 (23%)</td>
<td>216 (18%)</td>
<td>1543</td>
</tr>
<tr>
<td>Size at maturation</td>
<td>288 (74%)</td>
<td>1427 (30%)</td>
<td>267 (22%)</td>
<td>1982</td>
</tr>
<tr>
<td>Age at maturation</td>
<td>254 (65%)</td>
<td>1178 (25%)</td>
<td>219 (18%)</td>
<td>1651</td>
</tr>
<tr>
<td>Fecundity</td>
<td>314 (81%)</td>
<td>1189 (25%)</td>
<td>245 (20%)</td>
<td>1748</td>
</tr>
<tr>
<td>Egg size</td>
<td>248 (64%)</td>
<td>820 (17%)</td>
<td>130 (11%)</td>
<td>1198</td>
</tr>
</tbody>
</table>
common name or other possible ‘older’ nomenclature. Third, data were obtained from electronic databases (e.g., FishBase; Froese & Pauly, 2015). Values for size and age at maturation were recorded for female specimens when data were reported for both sexes. Mean values of reported trait values were used when multiple data sources were available. By doing so, intra-specific trait variability was implicitly considered as negligible compared with inter-specific trait variability. This assumption is supported by Blanck and Lamouroux (2007) who demonstrated that life-history traits related to fecundity and body size varies more between than within species for freshwater fishes in Europe.

Next, species were classified into one of three categories according to their distributional status at the global scale. Invasive species (n = 388) were those with known established populations outside their country or countries of origin based on a comprehensive review of published literature and online databases (Olden, unpublished data). Threatened species (n = 1210) were those categorized as Critically Endangered (CR), Endangered (EN) or Vulnerable (VU) according to the Red List of Threatened Species (IUCN, 2015, version 4; http://www.iucnredlist.org). Native species (n = 4695) included species considered neither invasive nor threatened. Species classified as both invasive and threatened species were excluded from the database.

The final database contained 240 families and 1796 genera, for a total of 14,415 trait values. The mean proportion of missing trait values in the database varied from 27% for invasive species to 66% and 70% for native and threatened species, respectively (Table 1). Missing data are a common problem in meta-analysis, as it may compromise inferences by reducing precision and biasing the results (Blackburn & Jeschke, 2009; Rypel, 2014). Here, missing values undoubtedly reduced the power to detect trait differences among invasive, native and threatened species. Although unfortunate, the level of completion of the database reflects the current state of knowledge regarding the life-history characteristics of freshwater fishes for which information in some regions (e.g., Southeast Asia, South America) are seldom available. This may be especially problematic for threatened species owing to the difficulties in sampling often small and locally rare populations. Nevertheless, the proportion of missing values also varies according to the trait considered. For instance, maximum body size was available for all 6293 freshwater fish species, and as such was not likely to suffer from any taxonomic or spatial biases. Finally, in order to alleviate the influence of potential taxonomic imbalance because of the non-random distribution of missing values across species, all the analyses were restricted to congeneric species (see below). Although acknowledging these shortcomings, this study is based on the best available knowledge.

### 2.2 Data analysis

Differences in traits between invasive and native species and between threatened and native species were quantified using the unbiased effect size (Hedges’ d), which indicates the direction of the difference by its sign and the magnitude of the difference by its value (Hedges, Gurevitch, & Curtis, 1999). A positive value of d indicated that invasive or threatened species show larger trait values than native species. To account for phylogenetic inertia – that is, the fact that closely related species are more likely to exhibit similar characteristics than more distantly related species – calculation of effect size was restricted to congeneric species.

For each trait, effect sizes were calculated separately for invasive and threatened congeneric species as follows:

\[ d_i = \frac{(\overline{X}_{inv/\text{thr}} - \overline{X}_{nat})}{S} \]

where \( \overline{X}_{inv/\text{thr}} \) and \( \overline{X}_{nat} \) are the mean values for the invasive or threatened species and the native species belonging to the ith genus, respectively, S is the pooled standard deviation:

\[ s = \sqrt{\frac{(N_{inv/\text{thr}}-1)(s_{inv/\text{thr}})^2 + (N_{nat}-1)(s_{nat})^2}{N_{inv/\text{thr}} + N_{nat}-2}} \]

where \( s_{inv/\text{thr}} \) and \( s_{nat} \) are the standard deviations for the invasive or threatened species and the native species and N is the number of species in each group. J is a weighting factor:

\[ J = \frac{1}{4(N_{inv/\text{thr}} + N_{nat}-2)} \]

The mean effect size (\( d \)) was then calculated by weighting the effect sizes of different genera by the inverse of their squared standard error (\( w_i \)) following Lipsey and Wilson (2001):

\[ w_i = \frac{1}{\left( \sqrt{\frac{N_{inv/\text{thr}} + N_{nat}-1}{2(N_{inv/\text{thr}} + N_{nat})}} \frac{d}{s} \right)^2} \]

Confidence intervals of the mean effect size were estimated through a bootstrap resampling procedure using 4999 permutations (following van Kleunen et al., 2010). Differences in life-history traits were considered significant if the 95% bootstrap confidence interval of the effect size did not overlap zero (Adams, Gurevitch, & Rosenberg, 1997). Furthermore, consistency in the direction of the differences across genera was examined using a binomial test by comparing the proportion of positive and negative effect sizes with random expectations.

The two-sides-of-the-same-coin hypothesis was tested by comparing the direction and magnitude of the effect sizes between invasive and threatened species of the same genus. This approach accounted for the influence of shared phylogeny on trait differences. For each trait, potential differences in the magnitude of the effect sizes were tested using Wilcoxon tests and differences in the direction of the effect sizes were assessed using Fisher tests.

As invasiveness and imperillment of species may result from the interplay of multiple traits acting in synergy (Davidson et al., 2012; Olden et al., 2006), a multivariate analysis was conducted based on the effect sizes for invasive and threatened species. A permutational multivariate analysis of variance (perMANOVA; 999 permutations) was first used to assess potential differences in mean trait composition between invasive and threatened species (i.e. whether their mean positions differ in the multivariate trait space). The within-group dispersion (variance) in multivariate trait space between invasive and threatened species was then compared using a permutation test of multivariate
homogeneity of dispersions (PERMUTEST; 999 permutations) (Anderson, Ellingsen, & McArdle, 2006). Gower’s distance metric was used in a Principal Coordinate Analysis (PCoA) to account for missing trait values; genera with only one trait effect size were omitted from the analysis. All the analyses were performed in R 3.2.0 (R Development Core Team, 2014) using the packages boot (Canty & Ripley, 2015), compute.es (Del Re, 2013), cluster (Maechler, Rousseeuw, Struyf, Hubert, & Hornik, 2015) and vegan (Oksanen et al., 2015).

3 | RESULTS

Life-history traits of invasive species were significantly larger compared with native species, with the exception of egg size (a measure of parental investment into juvenile survival) that showed no significant difference (Figure 1). Similarly, the directions of effect sizes were not randomly distributed across genera for all traits but egg size (binomial test; Table 2). Invasive species were characterized by larger body size, greater longevity, greater size and age at maturation, and higher fecundity compared with their congeneric native species. By contrast, there was only limited evidence that the life-history characteristics of threatened species differed from native species. Threatened species were characterized by shorter longevity and younger age at maturation, but longevity was the only trait significantly different from native species (Figure 1). The directions of the effect sizes were also all randomly distributed (binomial test, all P > 0.05; Table 2), indicating that there was no consistency in the direction of the effect sizes across genera.

Comparison of effect sizes between invasive and threatened species supported the two-sides-of-the-same-coin hypothesis. Univariate trait analyses showed that four out of the six traits – maximum body size, longevity, age at maturation and fecundity – significantly differed in both magnitude (Wilcoxon test, P < 0.05) and direction (Fisher test, P < 0.05) (Figure 2). Similarly, multivariate analyses demonstrated multi-trait differentiation between invasive and threatened species (perMANOVA, $F_{1,15} = 9.21, P < 0.01$). Within the two-dimensional space of the PCoA (68.2% of the original trait variance explained), invasive species were located on the left side, representing large body size, great longevity, delayed maturation and high fecundity, whereas threatened species were located on the upper-right corner, associated with small body size, short longevity, early maturation and lower fecundity (Figure 3). Invasive species also displayed a higher dispersion within the multivariate trait space than threatened species (PERMUTEST, $F_{1,17} = 4.13, P < 0.05$). The multivariate results were relatively insensitive to the varying number of missing trait values among species. Significant trait differences between invasive and threatened species were maintained regardless of whether all species included in the analysis had one (n = 257 species; perMANOVA, $F_{1,9} = 7.81, P = 0.004$), two (n = 276 species; perMANOVA, $F_{1,11} = 11.7, P = 0.003$) or three (n = 348 species; perMANOVA, $F_{1,15} = 7.04, P = 0.008$) out of six missing trait values.

![Figure 1](image1.png)

**FIGURE 1** Mean effect sizes (Hedges’ $d$) of life-history trait differences for threatened versus native congeneric species and for invasive versus native congeneric species. 95% confidence intervals are indicated as the error bar around the mean.

![Figure 2](image2.png)

**FIGURE 2** Pairwise comparison between effect sizes (Hedges’ $d$) of life-history trait differences for invasive versus native congeneric and threatened versus native congeneric species. Associated significance for binomial tests comparing the proportions of positive and negative effect sizes with random expectations are also reported. Positive effect sizes are indicated as '+' and negative effect sizes are indicated as '-'.

**TABLE 2** Direction of the effect sizes (Hedges’ $d$) of life-history trait differences for invasive versus native congeneric and threatened versus native congeneric species. Associated significance for binomial tests comparing the proportions of positive and negative effect sizes with random expectations are also reported. Positive effect sizes are indicated as '+' and negative effect sizes are indicated as '-'.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Invasive</th>
<th>P</th>
<th>Threatened</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maximum body size</td>
<td>8 / + 36</td>
<td>0.01</td>
<td>66 / + 49</td>
<td>0.14</td>
</tr>
<tr>
<td>Longevity</td>
<td>5 / + 15</td>
<td>0.04</td>
<td>15 / + 7</td>
<td>0.13</td>
</tr>
<tr>
<td>Size at maturation</td>
<td>6 / + 17</td>
<td>0.03</td>
<td>12 / + 15</td>
<td>0.70</td>
</tr>
<tr>
<td>Age at maturation</td>
<td>5 / + 17</td>
<td>0.02</td>
<td>17 / + 7</td>
<td>0.06</td>
</tr>
<tr>
<td>Fecundity</td>
<td>4 / + 14</td>
<td>0.03</td>
<td>14 / + 7</td>
<td>0.19</td>
</tr>
<tr>
<td>Egg size</td>
<td>9 / + 6</td>
<td>0.61</td>
<td>6 / + 7</td>
<td>0.99</td>
</tr>
</tbody>
</table>
In support of the two-sides-of-the-same-coin hypothesis this study provides strong evidence that globally invasive and threatened freshwater fishes are positioned at distinct and opposite locations along a continuum of life-history strategies. Invasive species generally reach larger maximum body sizes, demonstrate delayed maturity, and are longer-lived with higher fecundity. These attributes are characteristic of both periodic and equilibrium life-history strategists (sensu Winemiller & Rose, 1992). Periodic species are favoured in seasonal, periodically suitable environments with large spatial (patchiness) and temporal (seasonality) heterogeneity, while equilibrium strategists typically inhabit environments with low variation in habitat quality and strong biotic interactions (Mims & Olden, 2012; Winemiller, 2005). By contrast, threatened species typically achieve smaller maximum body sizes, mature at younger ages, and are shorter-lived with relatively low fecundity. Species exhibiting these attributes are typical of opportunistic life-history strategists, favoured to occupy habitats subjected to frequent and intense disturbances.

These results are consistent with findings of other studies reporting strong trait associations with invasion and extinction risk (Capellini et al., 2015; Olden et al., 2006; Sæther et al., 2004; van Kleunen et al., 2010), but differ from studies on other major taxonomic groups in terms of the direction. For instance, large body size has been linked repeatedly to elevated extinction vulnerability in various vertebrate groups, including mammals (Davidson et al., 2009), birds (Jeppsson & Forslund, 2012) and marine fishes (Olden, Hogan, & Vander Zanden, 2007), and short generation time was reported to be associated with higher invasion risk (Rosenicchi, Thomas, & Crivelli, 2001). This discrepancy may be attributable partly to the widespread intentional introductions of large-bodied fishes for commercial and recreational purposes (Cucherousset & Olden, 2011), a pattern documented for freshwater fish at a global scale (Blanchet et al., 2010). Beyond human factors, these results may also be explained by species’ biological performances. With high fecundity and extended longevity, invasive species may exhibit high propagule pressure, show fast population growth and cope with lengthy periods of adverse conditions in their introduced range, thus accelerating successful establishment and subsequent spread. By contrast, short generation times coupled with relatively low fecundity of threatened species may be related to higher demographic stochasticity, conferring them lower resilience to environmental change (Olden et al., 2007; Olden, Poff et al., 2008).

Strong support for the two-sides-of-the-same-coin hypothesis in the present study contradicts the cross-continental comparison of Blackburn and Jeschke (2009) who found only limited evidence for trait differences between invasive and threatened freshwater fish. Such discrepancy may arise from differences in taxonomic composition and number of species considered; global (this study) versus Europe and North America (Blackburn & Jeschke, 2009). Perhaps more importantly, the trait comparisons between congeneric invasive, native and threatened species were restricted, thus accounting for the confounding influence of phylogeny and potential taxonomic imbalance caused by missing trait information (Alcaraz, Vila-Gispert, & García-Berthou, 2005; García-Berthou, 2007). Nonetheless, despite multivariate trait differences between invasive and threatened species (supporting the two-sides-of-the-same-coin hypothesis), invasive species displayed considerably greater trait diversity compared with threatened species. This may simply reflect the fact that invasion success is not related to any single trait, but rather reflects different traits operating at different stages of the invasion process from introduction to establishment (Marchetti et al., 2004). By contrast, a smaller, and more specific combination of traits may predispose freshwater fishes to eventual extinction. Despite being subject to a large range of threats, such as habitat degradation and extensive harvesting, whose effects may be difficult to predict (Reynolds et al., 2005; Olden et al., 2006, 2007), similar traits may operate across multiple stages of extinction (from rarity to extirpation to extinction), resulting in more limited trait variation (Olden, Poff et al., 2008).

As with any macro-ecological study, it is important to recognize and discuss potential methodological limitations. First, missing data for some traits may have resulted in reduced statistical power for analysis; however, missing data were shown to have no influence on the major findings. Second, this study considered mean trait values at the species level, thus they did not account for the role of intraspecific trait variability. Although interspecific trait differences are likely to dwarf intra-specific trait differences given the taxonomic diversity of the study, invasive species may exhibit significant trait differentiation during the invasion process (Liu et al., 2015). Despite these limitations, this study shows that life-history traits are highly indicative both of invasion and extinction risk in freshwater ecosystems. More advanced indicators of extinction and invasion risk would therefore incorporate intra-specific trait variability and explicitly consider the specific mechanisms by which traits may confer risk (Olden, Poff et al., 2008).

The International Union for Conservation of Nature (IUCN) Red List remains the most authoritative system available for classifying the risk of extinction of a species, yet time and resources are too limited to collect the necessary data for all species to be assessed (Bland, Collen, Orme, & Bielby, 2015). Among the different approaches to overcome this challenge, recent studies have modelled correlations between existing species’ trait data and extinction risk among data-sufficient species to predict the conservation status of data-deficient species.
species. For example, Bland, Orme, et al. (2015) described the potential utility of trait-based predictions to support the Red List assessment process and allow a more systematic way of assigning priorities to species to be considered for evaluation. The present study contributes to this growing area of research by demonstrating that trait-based approaches allow the rapid classification of extinction risk for freshwater fishes, and may ultimately inform species conservation assessments at regional, national, and global scales (Olden et al., 2010).

Similarly, risk assessments based on species traits can offer scientifically rigorous support for efforts at preventing invasion (Capellini et al., 2015). Aggregating species assessment results across specific invasion pathways or regions can help decision-makers determine which species and sources of emerging invaders deserve greater management or policy attention (Howeth et al., 2016). Trait-based models, such as the one presented here for global freshwater fishes, can help conservation efforts move from reactive to proactive strategies by identifying species that pose high invasion risk before they become established and spread into new areas.

Freshwater fishes are one of the most imperilled faunas in the context of escalating human pressures (Almeida & Grossman, 2014; Reynolds et al., 2005). Increasing human-mediated species invasions and extinctions are motivating the development of cost-effective conservation strategies for identifying species with greater risk of invasion and extinction (Gozlan, Britton, Cowx, & Copp, 2010; Olden et al., 2010). This study highlights the importance of understanding species' life-history traits to assess their invasiveness and vulnerability. We find global support for the two-sides-of-the-same-coin hypothesis whereby invasive and threatened freshwater fishes exhibit markedly different life-history strategies. Trait-based approaches can support conservation practitioners as they seek to develop more proactive management strategies in the future.

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REFERENCE