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Relative importance of exotic species traits in determining invasiveness across levels of establishment: Example of freshwater fish

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Abstract

1. Understanding the factors responsible for the success of exotic species is a prevalent issue in invasion biology. Although the ecological traits of exotic species are known to play a major role, it is still unknown which traits are responsible for the different dimensions of invasiveness among vertebrates.
2. Here, we assessed the ecological, morphological and behavioural profile of 222 exotic freshwater fish along different levels of establishment, defined by the number of basins in which the exotic species are established and the location of establishment. Using a trait-based multidimensional space complemented by a trait-by-trait analysis, we attempted to classified exotic vertebrates given their intrinsic traits across establishment levels ranging from species with low establishment to super-established species.
3. We found that fish with low establishment were clustered in the trait space, showing similar traits characterized by low-temperature amplitude, no parental care and zoobenthic diet. By contrast, super-established fish had a broader range of functional strategies, with a high proportion of species having multiple diets and a high level of parental care. Overall, fish with low establishment had low functional overlap with other fish at higher levels of establishment.
4. Our findings highlight the importance of considering trait variability in the species' level of establishment to more accurately anticipate their ability to establish and spread.

KEYWORDS

establishment success, exotic fish, exotic range, traits, vertebrates

1 | INTRODUCTION

To date, the overwhelming majority of countries throughout the world are home to exotic species (Dawson et al., 2017). The current rise in new exotic species introductions is set to amplify

the phenomenon of biological invasion in the future (Seebens et al., 2021). Understanding why some exotic species become established in a new location while others fail remains a challenging question (Enders et al., 2020). Studies have shown that the success of exotic species depends on a combination of different factors

Camille Bernery and Clara Marino contributed equally to this work

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involving propagule pressure, the biotic characteristics of the recipient ecosystem and exotic species traits (Allen et al., 2017; Bernery, Bellard, Courchamp, Brosse, & Leroy, 2022; Blackburn et al., 2009; Capellini et al., 2015; Marino & Bellard, 2023; Novoa et al., 2020). For instance, reptiles and amphibians established in exotic environments have larger or more frequent clutches compared with species that fail to establish (Allen et al., 2017). Exotic birds that are successfully established mostly present slow life-history traits (e.g. large body mass and low brood value; Sol et al., 2012), while those with high ecological impacts have large clutch sizes (Marino & Bellard, 2023). In addition, exotic freshwater fish with a broad food spectrum have a greater chance of establishing than species with more specialized diets (Ruesink, 2005), although this varies with the stage of invasion (Bernery, Bellard, Courchamp, Brosse, Gozlan, et al., 2022). Among other factors, species traits play an undeniable role in the establishment process.

However, not all exotic species are equally successful at invading new ecosystems. Some species will establish in many locations and spread widely such as the black rat *Rattus rattus*, which has established populations in 417 islands around the world (Threatened Island Biodiversity Database Partners, 2018), and the common carp *Cyprinus carpio*, which has established populations in 730 basins worldwide (Tedesco et al., 2017). Nevertheless, other species remain limited to a specific location such as the lesser rice field rat *Rattus losea*, which is established in only four islands in the Taiwan Strait (Threatened Island Biodiversity Database Partners, 2018). As widespread and impactful exotic species lie at the core of management strategies, it is crucial to consider the different dimensions of species invasiveness (Catford et al., 2016). Recent studies have demonstrated that exotic range size, exotic species abundance and impact on native fauna are dimensions of invasiveness (Catford et al., 2019; Liao et al., 2021). When applied to exotic plants, these dimensions were found to be independent and differentially related to exotic plant traits. For example, leaf nitrogen content and leaf area were more strongly associated with exotic range size, while leaf dry weight was more correlated with the local abundance of exotic plants (Liao et al., 2021). Nevertheless, it is unknown how trait associations vary along different levels of invasiveness in animal taxa. Overlooking apparent distinctions in the dimensions of invasiveness can lead to inconsistent conclusions about the factors responsible for establishment success (Liao et al., 2021).

Freshwater fish are one of the most frequently introduced taxa worldwide and are known for their strong impact on native fauna (Cucherousset & Olden, 2011). Yet this taxon is less studied in terms of the factors influencing their invasion success than other vertebrate taxa (Pyšek et al., 2020). Previous studies identified traits and characteristics impacting the establishment success of exotic freshwater fish for specific regions or a restricted sample of species (e.g. Ribeiro et al., 2008; Tonella et al., 2018). For instance, Marchetti et al. (2004) and Drake (2007) both highlighted the importance of a strong parental care to successfully establish, in California or for 39 species worldwide, respectively. Peoples and Midway (2018) showed that the size of the native range and the fishing and aquaculture use,

linked with several functional traits (e.g. diet, body shape and temperature range), influenced the number of watershed in the eastern United States where the exotic fish established. At the global scale, Su et al. (2020) showed that among established fish species, species exported outside their native range had more extreme morphological traits than species translocated within the same realm. Yet, they did not take into account ecological (e.g. temperature amplitude) and behavioural factors (e.g. parental care) that could contribute to explaining species establishment.

Here, we aimed to disentangle the effects of 13 ecological, morphological, and behaviour factors associated with two dimensions of exotic freshwater fish establishment for 222 species worldwide: The number of basins in which the exotic species are established (as a proxy for exotic range size) and the location of establishment (i.e. inside or outside the native bioregion). Considered together, these dimensions form different levels of establishment (Figure 1), ranging from species established in just a handful basins within their native bioregion (i.e. species with low establishment) to exotic species that are successful widespread over several basins, including some beyond their native bioregion (i.e. super-established species). Using a trait-based multidimensional space complemented by a trait-by-trait analysis, we attempted to classify exotic vertebrates across establishment levels given their intrinsic traits. We evaluated the similarities and dissimilarities between groups of exotic fish using density distributions along the axes of the functional space, further completed with a probabilistic hypervolume approach (Mammola et al., 2021; Mammola & Cardoso, 2020). We aimed to disentangle the most successful invaders (i.e. 50% that perform better than others) compared to the rest of fish and to test if some traits are associated with levels of establishment. More precisely, we expect fish with a high establishment level to have good swimming abilities, a broad temperature tolerance, a high level of parental care and a generalist diet (Bernery, Bellard, Courchamp, Brosse, Gozlan, et al., 2022; Carvajal-Quintero et al., 2019; Lawson & Hill, 2022; Ruesink, 2005; Snyder et al., 2014; Su et al., 2020; Tonella et al., 2018).

2 | MATERIALS AND METHODS

2.1 | Species data

Using a global database of freshwater fish species distribution (Tedesco et al., 2017), we compiled a list of freshwater fish (i.e. freshwater recorded as one of their habitats in FishBase; Froese & Pauly, 2019), which were defined as exotic in at least one drainage basin ($n=547$). In this study, exotic species are defined as introduced species that have become established and completed their entire life cycle with a self-sustainable population in a given basin outside their native range. We then collected information on the exotic fish regarding their level of establishment as well as their life-history traits (Brosse et al., 2021; Froese & Pauly, 2019). All the analyses were performed on a set of 222 established exotic freshwater fish for which we had complete data for these variables (see the Section 2.1.2 below).

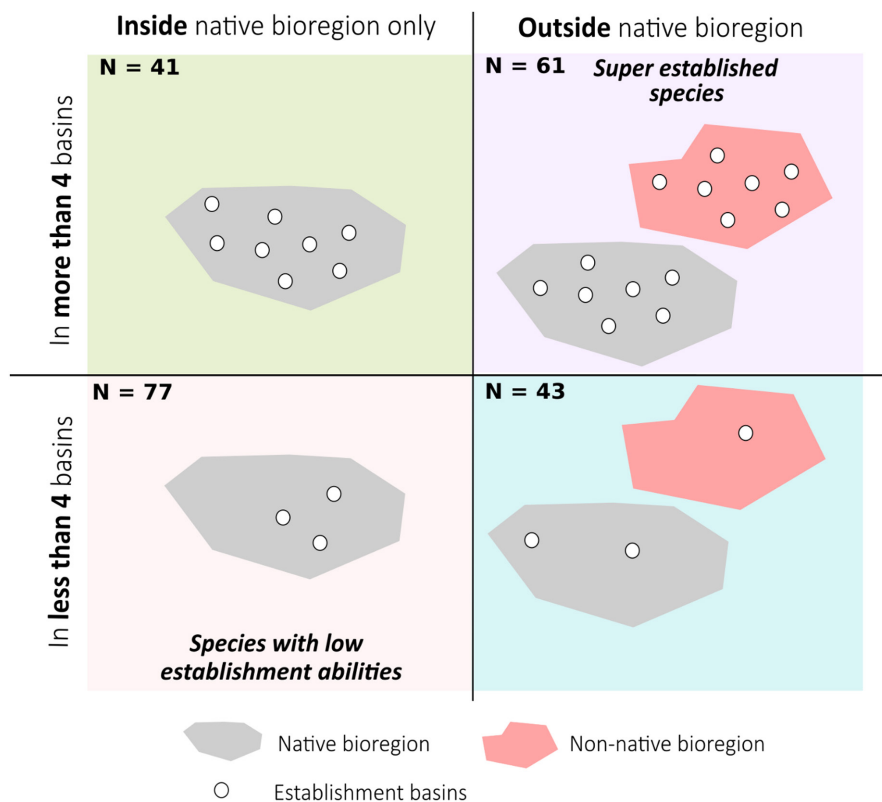


FIGURE 1 Schematic representation of the different fish groups according to their establishment level. The white circles represent the drainage basins where the species are established. Grey areas represent the native bioregion, and red areas the non-native bioregion.

2.1.1 | Species exotic distributions

We collected information on the two dimensions of the establishment levels for each exotic fish: (i) the number of basins in which the species is established and (ii) the location of establishment. For the number of basins, we counted the number of drainage basins where the species have an exotic status using the database of Tedesco et al. (2017). We further separated fish species into two categories: species established in four or less basins and those established in more than four basins. The cut-off of four corresponds to the median number of basins for the 222 species (see Table S1 in Supporting Information for the sensitivity analysis of the cut-off). Regarding the location of the exotic establishment, we also distinguished two groups following the bioregion classification of Leroy et al. (2019): species that were only introduced and established in their native bioregion(s) and species that were introduced outside their native bioregion(s) (even if they could also be introduced inside it). Among the 222 exotic species, 120 were established in four or less basins, while 102 were found in more than four basins; 118 species were established only inside their native bioregion, while 104 had an established population outside it. Based on these two dimensions of establishment, we constituted four groups of fish (Figure 1). The levels ranged from species with low establishment with low values for both dimensions (i.e. number of basins and location of establishment) to super-established fish species with high values for both dimensions. We defined two intermediary groups that had a low value for one dimension but a high value for the other.

2.1.2 | Species traits

Based on previous research, we collected information on 13 ecological, behavioural and morphological species traits likely to facilitate the establishment of freshwater fish (Table S2). Regarding the ecological traits, we collected diet data using the 'Foodl' column of the *fooditems()* table of the *RFISHBASE* package (Boettiger et al., 2012; Froese & Pauly, 2019). Each species can have one or several diets belonging to five categories (i.e. detritus, nekton, plants, zoobenthos and zooplankton), so we transformed the 'Foodl' variable into five binary variables according to the five diet categories. We also counted the number of diet categories for each species to determine their diet breadth. We then calculated the temperature amplitude of each species. For this purpose, we retrieved the minimum temperature of the coldest month and the maximum temperature of the hottest month in the native basins of species from Worldclim (Fick & Hijmans, 2017). We only considered the 0.95 quantile of the maximum temperature of the hottest month and the 0.05 quantile of the minimum temperature of the coldest month to avoid extreme outlier values.

We obtained information on the behavioural traits such as fish parental care using the 'RepGuild1' column of the *species()* table of the *RFISHBASE* package (Boettiger et al., 2012; Froese & Pauly, 2019). The parental care variable was divided into three categories from the lowest to the highest level of parental care: non-guarder, guarder and bearer.

Regarding the morphological traits, we considered five variables from the *FISHMORPH* database (Brosse et al., 2021). First, we used the pectoral fin vertical position *PFiBd* (i.e. ratio of pectoral fin position relative to body depth), which reflects the swimming style.

Lateral pectoral fins are used for propulsion and fine movements, whereas ventral pectoral fins often characterize fish with less precise movements (Blake, 2004; Su et al., 2019). Second, we used the ratio of body length to body depth (BIBd), which reflects fish hydrodynamics (Su et al., 2019; Villéger et al., 2017). Third, we used the ratio between the eye position and body depth (EhBd), which indicates the 'position of the fish and/or its prey in the water column' (Su et al., 2019). Fourth, we used the ratio between the oral gape position and body depth (MoBd), thus showing the feeding position of the species in the water column (Su et al., 2019). Finally, we used the maximum body length of the species (in cm). We obtained these trait data for 222 exotic fish species. All details on traits are summarized in Table S2. We also gathered information on species phylogeny at a categorical level by retrieving their Genus, Family and Order from the `load_taxa()` table of the `RFISHBASE` package.

2.2 | Statistical analyses

2.2.1 | Building trait space

To ensure that the traits were not intercorrelated, we regressed each trait against all others using linear models and then computed the variance inflation factors (VIF) using the `vif()` function from the `CAR` package (Fox & Weisberg, 2019). As diet breadth was aliased with other diet variables, we did not consider this trait in the remainder of the analyses. Indeed, we considered only 12 traits for which VIF values were less than 3 for all the remaining variables. We then used the 12 traits of the 222 fish species to build a multidimensional trait space. First, we calculated the synthetic axes that provide new species coordinates in a low-dimensional space using the `funct.dist()` and `quality.fspace()` functions from the `MFD` package (Magneville et al., 2021). The first function computes pairwise trait-based distances between species using the Gower dissimilarity index (Gower, 1971), which permit to consider different types of traits (i.e. continuous numeric, discrete numeric and categorical traits). The second function calculates species coordinates in a multidimensional space by applying principal coordinate (PC) analysis (PCoA) and measures the quality of spaces according to the number of dimensions. A functional space is of good quality when the Euclidean distance between each pair of species in the multidimensional space constituted by the PC axes is close to the initial Gower's distance. We thus calculated the mean square deviation (mSD, Maire et al., 2015) between the initial Gower's distance and the Euclidean distance in each of the functional spaces (with three, four or more dimensions). We then retained the functional spaces that have the smaller mSD, that is, the functional space giving the more accurate representation of functional distances between species. The smaller mSD was obtained for the 4D trait space (mSD=0.046), so we kept the first four PC axes to pursue the analyses. Finally, we explored the correlations between the 12 traits and the four PC axes by calculating Spearman coefficients. The only non-numeric trait (parental care) was converted into an ordered factor from the lowest level of parental care to the highest: 1=non-guarder, 2=guarder, 3=bearer.

2.2.2 | Functional distinction of species along the dimensions of the establishment levels

To assess the functional differences between the groups of fish according to the number of establishment basins and the location of establishment, we compared the between-group distribution along the PC axes using Kolmogorov–Smirnov tests, which were run independently for the number of basins (four or less vs. more than four) and the location of establishment (inside vs. outside native bioregion). To determine whether the results were sensitive to the group definition, we repeated the same analyses for different thresholds regarding the number of basins (cut-off = 2, 3, 5 and 6 basins). As the results obtained for the groups of small and large numbers of basins at different cut-offs corresponded to the cut-off of four basins (Table S1), we retained the cut-off of four basins for the rest of the analyses. To explore the influence of species grouping and cut-off on the results, we built a generalized linear model on the continuous variable 'number of establishment basins'. The method and results of this analysis are presented in Appendix 2.

2.2.3 | Hypervolume comparison along the establishment levels

We further proceeded to a dissimilarity analysis of the probabilistic hypervolumes of each group in the 4D trait space. The following functions for the computing hypervolumes and associated metrics were taken from the `BAT` package (Cardoso et al., 2022). We first built kernel density hypervolumes with the `kernel.build()` function using the first four axes of the PCoA as traits and the four groups of fish across the establishment levels as groups. We used the Gaussian kernel density method and kept the default parameters (Blonder et al., 2018). Second, we calculated the pairwise distances between the hypervolume centroids (with six two-by-two distances) using the `kernel.similarity()` function. Then, to estimate how the four groups were dissimilar in terms of their trait space occupation, we computed pairwise hypervolume dissimilarities between the groups using the `kernel.beta()` function. Total beta dissimilarity was further decomposed into replacement (beta replacement) and gain or loss in richness (beta richness), which, respectively, describe the shift in the functional space and the expansion or contraction between two given groups. Finally, we tested whether the observed distances and dissimilarities between groups were significantly higher or lower than expected by chance. With this aim, we randomly attributed species to one of the four groups of the levels and calculated each metric. We obtained null distributions of 999 simulated values and calculated the deviation from random expectation by measuring the effect sizes and associated p-values following Marino et al. (2022). We considered an observed value to be significantly different from random expectation when it was above 97.5% or below 2.5% of the simulated values (resulting in a significance level of 5%).

2.2.4 | Individual trait distinctions across the establishment levels

We evaluated the trait modalities or values associated with the four studied groups. For each numeric trait, we compared the mean value of the groups using Wilcoxon and post hoc tests. For binary and categorical traits, we performed nonparametric chi-squared tests of independence. We also ran a non-parametric chi-squared test based on the Order to test the potential interaction between the establishment level and the taxonomy.

All analyses were performed with R software (version 4.1.0; R Core Team, 2022).

3 | RESULTS

3.1 | Functional qualification of fish on the two dimensions of the establishment levels

The first four axes of the functional space represented 65% of the total variance of the traits described for the 222 exotic freshwater fish species (Figure 2, Table S3). The two first axes were essentially driven by diet traits: PC1 was mostly associated with plant and detritus feeding, whereas PC2 was positively associated with nekton

and zooplankton feeding. PC3 was positively associated with a high level of parental care and negatively correlated with the temperature amplitude. Finally, PC4 was also associated with diet traits (i.e. negatively associated with zooplankton but positively associated with plant and nekton feeding) in addition to swimming ability (i.e. vertical pectoral fins).

We found that exotic fish had a different distribution along the first three axes of the functional space regarding both dimensions of establishment (Figure 2). For instance, fish established in more than four basins are more likely to feed on zooplankton, plant and detritus compared with other exotic fish (Figure 2, blue curves; see Table S4 for statistical tests). Our results also showed that exotic fish with established populations outside their native bioregion were distributed in the functional space correlated with high parental care compared with exotic species only established within their native range (Figure 2, pink curves; Table S4).

3.2 | Fish with low establishment are functionally distinct from other fish groups

We further explored whether the functional space can provide insights into the (dis)similarities of exotic fish across levels of establishment (Figure 1). The hypervolume centroids representing each

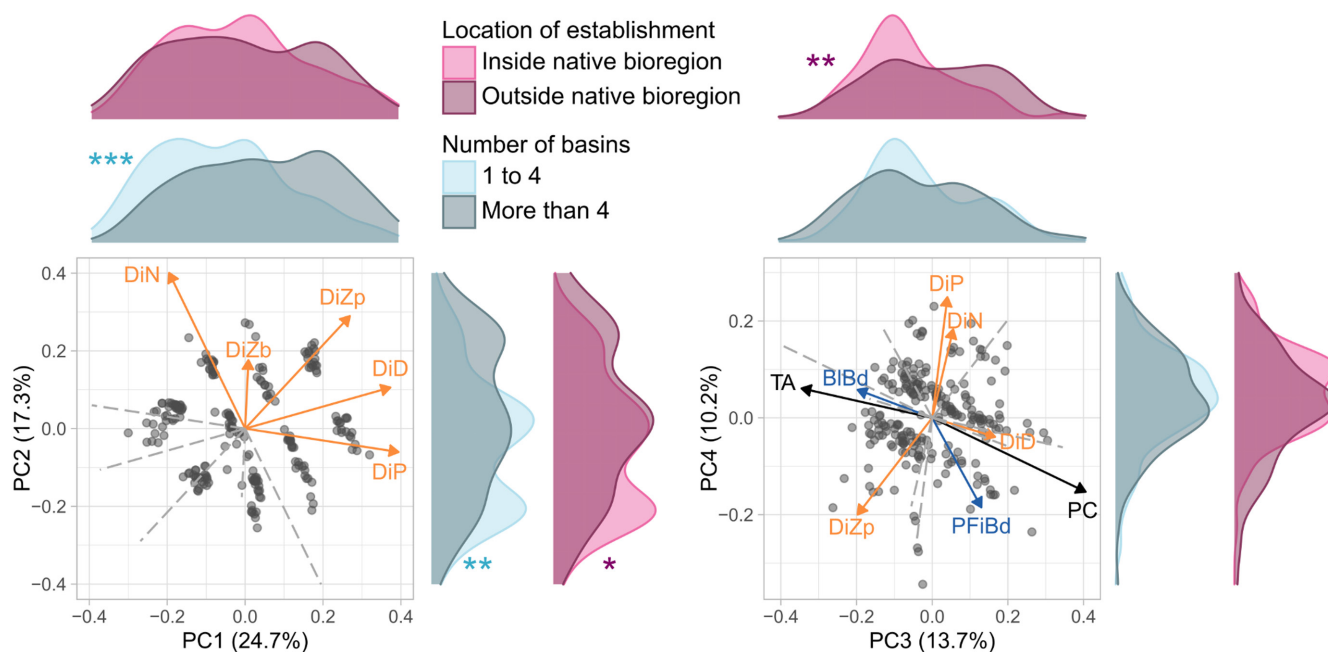


FIGURE 2 Functional space of introduced fish and repartition according to the location and number of introductions. The biplots represent the distribution of fish on the first four axes of the principal coordinate analysis. Each point depicts a species ($n = 222$), and arrows represent the traits that are the most correlated ($r > 0.3$) to the different axes (BIBq: body elongation, DiD, diet detritus; DiN, diet nekton; DiP, diet plant; DiZb, diet zoobenthos; DiZp, diet zooplankton; PC, parental care; PFiBd, pectoral fin vertical position; TA, temperature amplitude). Correlation coefficients and associated p -values are detailed in Table S3. Arrow colours correspond to the trait categories: diet (orange), morphology (blue) and parental care and temperature amplitude (black) as depicted in Figure 4. Distributions on the right and above the plot illustrate the density of species along the principal coordinate axes according to the location of establishment (pink curves) and the number of establishment basins (blue curves). Stars indicate that distributions are significantly different between groups following the Kolmogorov–Smirnov tests (*: $0.01 < p < 0.05$; **: $0.001 < p < 0.01$; ***: $p < 0.001$).

group were quite close in the functional space (Figure 3a). However, the observed distances in 4D space were higher than expected under a null hypothesis. In particular, fish with low establishment were significantly distant from fish established outside their native bioregion (Figure S1). We also observed that a large part of the functional space was shared by some groups across the levels (Figure 3b). Both groups of exotic fish established in more than four basins showed a high overlap (Jaccard index=0.61), as did both groups of exotic fish established outside their native bioregions (Jaccard index=0.62). Conversely, fish with low establishment had a Jaccard index of 0.35 with super-established fish. Indeed, the group of fish with low establishment systematically differed from the other groups due to the high beta richness. Despite containing numerous species ($n=77$), this group encompassed a smaller part of the functional space than any other group (Figures 1 and 3).

3.3 | Trait profile of exotic fish across the establishment levels

Ultimately, we explored the trait-by-trait differences between four groups of exotic fish across the establishment levels (Figure 4). We found that the traits were associated differently with the two dimensions of the establishment levels. The ability of species to spread

into a large number of basins was mostly associated with diet types and temperature amplitude, while parental care was more associated with the location of establishment. By contrast, morphological traits played an important role in explaining both the number of basins and the location of establishment.

More specifically, we found that super-established species had a higher feeding position in the water column, a longer body length and lateral pectoral fins and were also less hydrodynamic compared with species with low establishment. For example, *Abramis brama*, which is in the top 25% of the most established species, combine these three characteristics. Moreover, the super-established species had a more diverse diet with more detritus and zooplankton than species established in four basins or less. Overall, species established in a large number of basins consumed in proportion more diet items (i.e. plants, zooplankton, detritus) and had a greater temperature amplitude in their native basins than species established in a small number of basins. By contrast, species established outside their native bioregion tended to have lateral pectoral fins and showed greater parental care compared with species established only inside their native bioregion, which had ventral pectoral fins and non-guarder behaviour.

We tested the potential confounding effect of fish taxonomy by describing fish families and orders in each of the four groups. Despite the groups were represented by a variety of families and

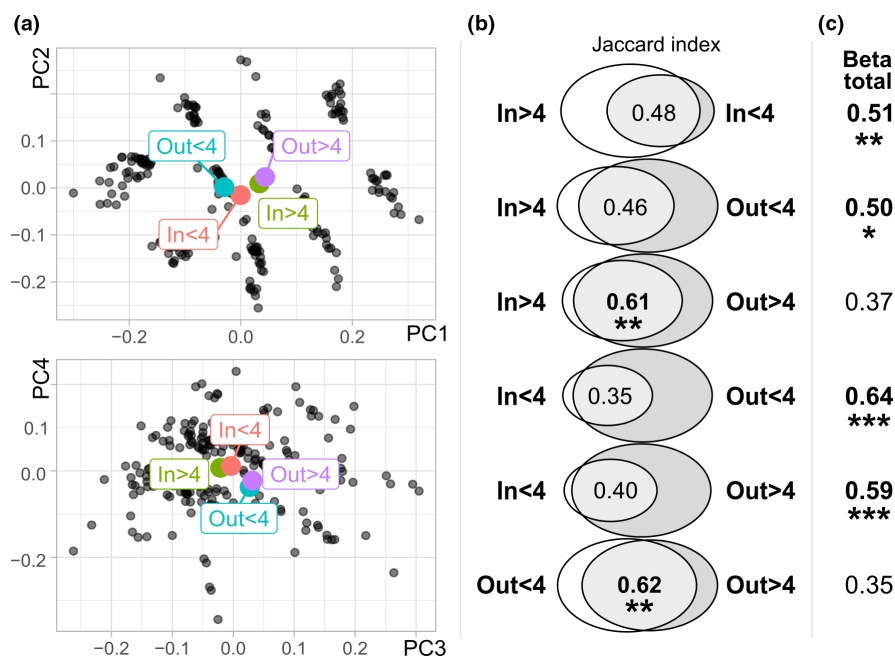


FIGURE 3 Distance, overlap and functional turnover between the four groups of introduced fish. The four groups correspond to the establishment levels: species introduced inside their native bioregion in four basins or less (In<4), inside their native bioregion in more than four basins (In>4), outside their native bioregion in four basins or less (Out<4) and outside their native bioregion in more than four basins (Out>4). The biplots (a) represent the functional space as in Figure 2, and the coloured points indicate the hypervolume centroid encompassed by each of the four groups. Venn diagrams (b) represent the functional overlap between hypervolumes (light grey) and the unique portions of the left (white) and right (dark grey) group. The Jaccard similarity index is specified in each intersection between groups. The table (c) indicates the differentiation (Beta total) between the two hypervolumes on the diagrams. Stars and bold values indicate the significant positive deviation from the null hypothesis, that is, the observed value is higher than expected by chance (** $p < 0.01$, *** $p < 0.001$, * $p < 0.05$).

orders, we highlighted a significant interaction between fish orders and establishment level ($\chi^2=90.5$, $df=48$, $p<0.001$; Figure S2A). The Cypriniformes were highly represented in the low establishment group, which was driven by the Leuciscidae family (Figure S2B).

4 | DISCUSSION

Our work demonstrated that ecological and behavioural traits contributed to determine fish's invasiveness across the dimensions of establishment (i.e. exotic range size and location), as previously shown for plants (Catford et al., 2016; Liao et al., 2021). For instance, diet and temperature amplitude were crucial in explaining the number of establishment basins as a proxy for exotic range size, while parental care had a greater effect on exotic location (Figures 2 and 4). Species with low establishment, which consumed zoobenthos and fed low in the water column, differed from super-established species, which were large generalist species with a broad temperature amplitude and a high level of parental care.

4.1 | Importance of traits to disentangle the dimensions of establishment in exotic species

Interestingly, all types of traits (ecological, morphological and behavioural) considered in our analyses influenced the establishment

of exotic fish, thus stressing the importance of considering all these variables when studying several dimensions of establishment success. This result demonstrates that focusing only on morphological traits (e.g. Su et al. (2020)) is insufficient to fully understand the different levels of establishment of freshwater exotic fish. Specifically, we demonstrated that traits represent either 'ecological drivers' of invasiveness because they confer a competitive advantage when colonizing the new environment (e.g. parental care) or 'societal drivers' because they make the fish more valuable to humans (e.g. body size). However, some traits were more important for disentangling the ability of the species to establish. The high level of parental care emerged as the main feature associated with exotic fish established outside their native bioregion. For example, the aquarium species *Gambusia holbrooki*, *G. affinis* and *Oreochromis mossambicus* were among the five most established species and were bearers (i.e. the higher level of parental care). We can assume that the high level of parental care facilitates fish reproduction in captivity, as it has been highlighted for ornamental marine fish (Moorhead & Zeng, 2010). Indeed, demersal spawners that display some degrees of parental care are more cultured, and thus more traded, because of their higher reproductive success in tanks. This behaviour has been positively selected in the ornamental industry and is thus more represented among introduced species worldwide. This result corroborates the findings of previous studies at more local scales, which observed a higher establishment success for exotic fish with a high level of parental care (Lawson & Hill, 2022; Marchetti et al., 2004), although they were unable to

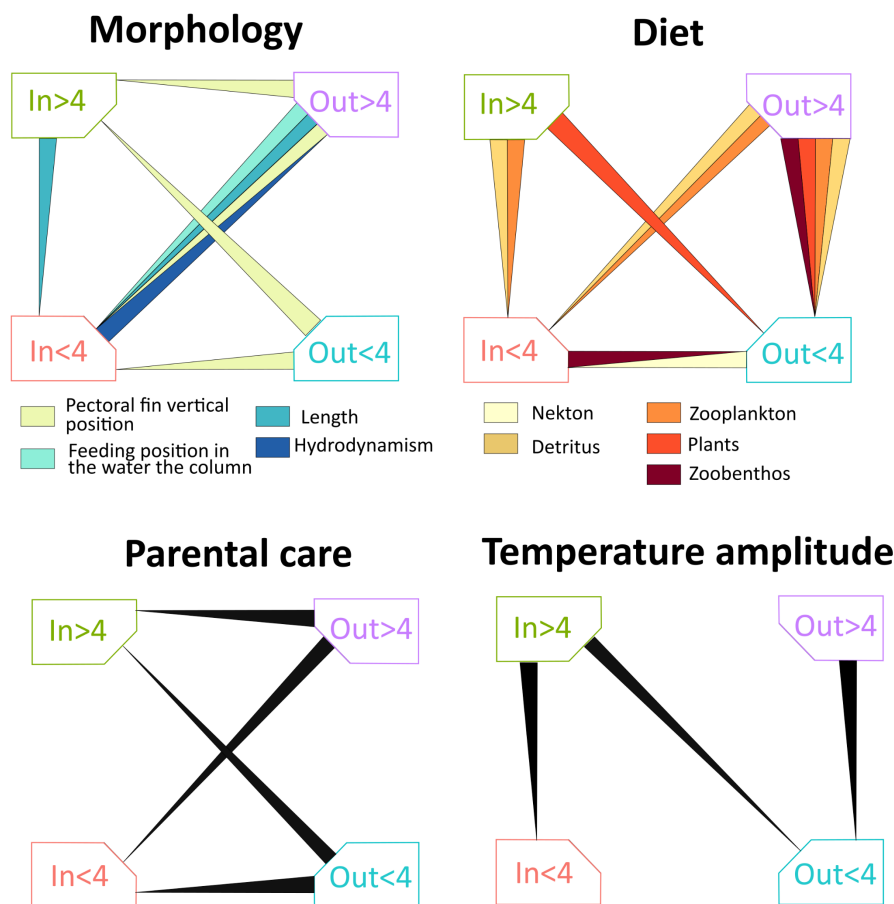


FIGURE 4 Trait comparison between the four groups of fish. The four groups correspond to the establishment levels: species introduced inside their native bioregion in four basins or less ($In < 4$), inside their native bioregion in more than four basins ($In > 4$), outside their native bioregion in four basins or less ($Out < 4$) and outside their native bioregion in more than four basins ($Out > 4$). Only significant differences are represented ($p < 0.05$). The group on the wide side of the triangle has higher values or is more represented in the considered trait compared with the other groups. Concerning the parental care panel, the group on the wide side of the triangle more significantly acts as bearers and guarders than the group on the narrow side of the triangle.

demonstrate a specific link between the location of establishment and parental care. For terrestrial vertebrates, parental care is often associated with slow life history. For example, Sol et al. (2012) demonstrated that exotic birds that had a slow life history and invested greater care in the next generation had more successful establishment compared with fast-living birds. By increasing the survival rate of offspring, parental care proves to be a critical trait in explaining establishment success and demography (Bernery, Bellard, Courchamp, Brosse, & Leroy, 2022; Marchetti et al., 2004).

Contrary to our expectations, we did not find any effect of temperature amplitude (as a proxy of temperature tolerance) to explain the ability of fish to establish outside their native bioregion. Most terrestrial exotic species from islands experience a niche shift after invasion, thus suggesting that their native climatic conditions are not a constraint to establishing outside their native realm (Stroud, 2021). As freshwater bodies are island-like systems (Itescu, 2019), the native range of fish might not correspond to their niche equilibrium, meaning that the climatic conditions experienced may be more limited than those that are tolerable (Lauzeral et al., 2011). For example, the realized niche of the catfish *Pterygoplichthys ambrosettii* extended by 27% in its exotic range (Frederico et al., 2019). Moreover, we considered the air temperature in our analysis while water temperature would have provided a more accurate view of fish ecological niche. However, we found that high-temperature amplitude in native basins was correlated positively with the number of establishment basins, as highlighted in previous studies (Kolar & Lodge, 2002; Marchetti et al., 2004; Snyder et al., 2014). This could be easily explained by the ability of species to adapt to different—and thus numerous—environments (Kolar & Lodge, 2002).

More surprisingly, we found that the number of basins was correlated with detritus and zooplankton diets. As detritus are not limited in the environment, detritivore species can easily find food resources without competing with native species (Tonella et al., 2018). In previous studies, nekton diets, which are associated with predatory behaviour on fish, were strongly linked with invasiveness (Moyle & Light, 1996; Tonella et al., 2018), although our study did not observe any effect of this diet.

Considering the two establishment dimensions together, the super-established fish were differentiated on account of the aforementioned traits as well as their morphology (Figure 4). Specifically, we found that super-established fish tended to be large with lateral pectoral fins (i.e. fins used for propulsion and fine movements) and a superior mouth type. Large fish, generally preferred by anglers and consumers, have been widely introduced worldwide through the aquaculture and fishery pathways (Bernery, Bellard, Courchamp, Brosse, Gozlan, et al., 2022). Because propagule pressure is a key factor associated with establishment success, we may expect that human preference for these species probably influences their higher success of establishment (Duggan et al., 2006; Lockwood et al., 2009). Moreover, the propulsion characteristic of lateral pectoral fins could be advantageous for dispersion, because it is associated with a more manoeuvrable body, which is beneficial in both slow and stagnant environments (e.g. for sneaking into vegetation),

thus favouring the establishment of fish in artificial environments such as dam or lakes (Dumay et al., 2004).

Species traits are intrinsically linked to phylogenetic history (Jetz et al., 2012), and the traits associated with the establishment levels were constrained by taxonomic organization of fish, specifically for the low-establishment group. Species from this group were mostly from the Leuciscidae family (order Cypriniformes) which could explain why the low-established species were more clustered than expected by chance in terms of traits. Species belonging to the Leuciscidae family tend to be small fish, which may be less attractive for commercial trade and fisheries, and therefore less transported and introduced compared to larger species.

4.2 | Potential contribution of socioeconomic factors to the establishment levels

Despite the trait differences between groups of exotic fish across the establishment levels, we found that all groups shared a large part of the functional space (at least 0.35 Jaccard index; Figures 2 and 3). Consequently, other drivers unrelated to the morphological, ecological and behavioural traits tested here might explain the distribution of exotic fish across levels. For instance, the local context of the invasions, including the invaded native community, is most likely to be a strong explanatory driver of establishment success due to both the functional and phylogenetic distances between exotic and native species (Xu et al., 2022). Native range size has also been demonstrated as an important determinant of establishment for both exotic fish and birds (Dyer et al., 2016; Marchetti et al., 2004). We could not use this variable in our study because data on the native range size were available only for 158 species upon the 222 we used (IUCN, 2022), hence reducing the statistical power of the analyses.

Moreover, the wide exotic distribution of certain fish could be explained by propagule pressure or the introduction pathways (García-Berthou et al., 2005). The frequency of introduction events and the number of individuals released per event affect establishment success during invasions, but it is almost impossible to have good proxies for these variables for fish on such a global scale (Bernery, Bellard, Courchamp, Brosse, Gozlan, et al., 2022). Plus, in aquatic systems, species introductions due to aquaculture and ornamental purposes facilitated the introduction and establishment of specific subsets of species worldwide (Padilla & Williams, 2004). In preliminary analyses, we separated the groups of fish according to the introduction pathway, although we did not find significant results. One possible explanation could relate to the limited number of fish species per pathway, thus strongly reducing the statistical power of analyses. Moreover, several fish species in our database such as the common carp have been introduced and established through several pathways, blurring the possible distinction expected between pathways.

Finally, the time since the first introduction into an exotic location may be correlated with establishment success, with a possible interaction with propagule pressure (Seebens et al., 2018). Indeed, the species that have been recorded as exotic for many centuries were

probably transported and introduced more frequently than species that have only recently been transported outside their native range. By testing the relationship between the establishment level and the first recorded date of introduction into an exotic place, we observed slight but nonsignificant support for this hypothesis (Figure S3). Indeed, the group of super-established fish tended to be detected earlier in an exotic place than the two groups of fish established in less than four basins. However, the number of fish with data in each group differed substantially, with a positive bias towards super-established species. This bias can be explained by the fact that widely invasive species with large impacts receive more attention and research.

4.3 | Link between establishment level and potential impact

In this paper, we focused on the dimensions of invasiveness related to the establishment stage of invasions, thus disregarding the ecological impact of species. However, this impact lies at the core of management strategies, because it determines the type of response implemented to counter the current or future invasion effects (McGeoch et al., 2021). Nevertheless, the paucity of data make it difficult to conduct large-scale studies (Bernery, Bellard, Courchamp, Brosse, Gozlan, et al., 2022; Thomsen et al., 2011). Moreover, it is highly challenging to quantify the impact of species in a standardized way (but see the EICAT framework in Blackburn et al., 2014; Hawkins et al., 2015). Ecological changes due to invasions and thus their impacts can go unnoticed for years or even decades, then hardly associated with invasions as responsible for those changes and impacts (Courchamp et al., 2017). However, theoretical frameworks suggest that the impact of an exotic species depends on three components: its exotic geographic range size, abundance and effect per capita (Latombe et al., 2022; Parker et al., 1999; Sofaer et al., 2018). Using the number of basins and the location of establishments as indicators of exotic geographic range, we can hypothesize that widely established exotic species are more likely to have a higher potential impact compared with species established in a small number of basins and restricted to their native bioregion. This has recently been demonstrated by Evans et al. (2018) for birds, in which species with large exotic range sizes tend to have more severe impacts than those with small exotic ranges. We tested this association (Figure S4) and found a significant correlation between super-established exotic species, which had high ecological impacts (i.e. 76% of them), whereas a small proportion of species with low establishment ability had ecological impacts (i.e. 17%). As a consequence, our results might serve as a preliminary attempt to characterize the impacts of exotic freshwater fish through indicators of establishment success.

4.4 | Study limitations

Although these results improve our understanding of invasion dynamics, it is crucial to consider the context of this analysis,

especially the data used, in order to acknowledge the limitations of our interpretations. We focus our analyses on the most comprehensive database of fish traits, which includes 222 traits with complete data (Brosse et al., 2021; Froese & Pauly, 2019), although over 300 exotic fish species have incomplete trait data, which prevented their inclusion in our analysis. We could have partially reduced this taxonomic bias by using imputation techniques based on phylogenetic information (Kim et al., 2018). However, the current phylogeny of Actinopterygii has undergone numerous changes and is not complete (Mirande, 2017). In addition, the high rate of missing values for the species traits (e.g. 127 of 547 species without the level of parental care, 146 species without the diet type) prevented us from using imputation techniques (Johnson et al., 2021). Global databases are often taxonomically and spatially biased towards developed countries, especially with regard to the distribution of exotic species (Bellard & Jeschke, 2016; Bernery, Bellard, Courchamp, Brosse, Gozlan, et al., 2022; Seebens & Kaplan, 2022). However, the pool of 222 exotic species considered here represented a fair subsample of the 547 species listed as exotic freshwater fish in the database of Tedesco et al. (2017). Specifically, the 222 species covered 2190 basins worldwide, whereas the 547 species were distributed in 2765 basins; the remaining 575 basins not covered by this paper were anecdotal in terms of their surface and number of exotic species (Figure S5). Ultimately, we acknowledge that the number of basins is only one possible metric to use for describing the establishment level. We selected this metric because of its availability across all species and because it reflects fish capacity to thrive in various freshwater environments. We choose to group species together, considering the median of the number of basins to separate them, and to not consider the continuous variable in order to test which factors are associated with the most successful invaders (above the median). The alternative would be to consider the number of establishment basins as a continuous response variable in a generalized linear model (GLM). The results of the GLM showed similar results regarding the variables that are associated with higher levels of establishment, but present different magnitude of the order of importance (see Appendix 2 for details). For instance, length was mostly associated with species that are established in a higher number of basins using the GLM, but with species that established outside their native range using the functional analyses. This could be due to the effects of some outliers species (e.g. *C. carpio* established in 731 basins and belongs to the 10% of the longest species). Note that Figure 4 also showed that alien fish established outside of their native region are more likely to show high parental care. By grouping species, we thus reduced the influence of species established in a high number of basins (Appendix 2, Figure S6). The effect of the size (as well as fecundity and propagule pressure) has also been demonstrated recently as a strong driver of invasiveness for >1800 North American freshwater fishes, while the diet and temperature-related traits had a moderate influence for this subset of species (Su et al., 2023).

5 | CONCLUSIONS

When assessing the species traits responsible for the establishment success of exotic vertebrates, previous studies considered establishment as a binary response, thus opposing successful versus unsuccessful species (Allen et al., 2017; Capellini et al., 2015; Ruesink, 2005; Sol et al., 2012). Our present study emphasizes the importance of considering the differences in species characteristics among established exotic vertebrates, with our fish model providing a better understanding of their invasion dynamics, as previously shown for plants (Catford et al., 2016, 2019; Liao et al., 2021). Ultimately, being able to identify the traits that promote the different levels of establishment of exotic species would help us to identify the most problematic invasive exotic species and thus help prevent their potential introduction and impacts.

AUTHOR CONTRIBUTIONS

Clara Marino, Camille Bernery and Céline Bellard conceived the ideas and designed the methodology; Clara Marino and Camille Bernery collected the data, analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

All authors declare that they have no competing interests.

DATA AVAILABILITY STATEMENT

The data and code that support our analyses are available from Zenodo (<https://zenodo.org/record/7982955>) and Github (https://github.com/claramarino/estab_levels_exotic_fish). Data include species traits and establishment characteristics.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Sensitivity to the cut-off of four basins for defining the two levels of number of basins. We evaluated the consequences of a cut-off change on the *p*-values evaluating the significance of the differences between each establishment outcome, for each axis of the PCoA. The four different groups correspond to the establishment levels: species introduced inside their native bioregion in four basins

or less ($\ln < 4$), inside their native bioregion in more than four basins ($\ln > 4$), outside their native bioregion in four basins or less ($\text{Out} < 4$), and outside their native bioregion in more than four basins ($\text{Out} > 4$). Significant p -values are represented in bold.

Table S2. Description of the traits used to describe the 222 exotic fish.

Table S3. Correlation between species traits and the first four axes of the principal component (PC) analysis containing the 222 exotic freshwater fish. Spearman coefficients and p -values are reported. The strongest correlations ($r < -0.4$ or $r > 0.4$) and their associated significant p -values are shown in bold.

Table S4. Results of Kolmogorov-Smirnov (KS) tests, their statistics (D) and associated p -values when comparing density distributions along the four axes of the PCoA for both dimensions of establishment.

Table S5. Results of the Chi-square tests evaluating the differences in proportion of species with ecological impact between groups along the levels of establishment. The four different groups correspond to the establishment levels: species introduced inside their native bioregion in four basins or less ($\ln < 4$), inside their native bioregion in more than four basins ($\ln > 4$), outside their native bioregion in four basins or less ($\text{Out} < 4$), and outside their native bioregion in more than four basins ($\text{Out} > 4$). In bold are statistically significant differences ($p < 0.05$).

Figure S1. Distances between centroids of the hypervolumes encompassed by the four groups of fish along the establishment levels. The four groups correspond to the establishment levels: species introduced inside their native bioregion in four basins or less ($\ln < 4$), inside their native bioregion in more than four basins ($\ln > 4$), outside their native bioregion in four basins or less ($\text{Out} < 4$), and outside their native bioregion in more than four basins ($\text{Out} > 4$). The orange square represents the observed value of distance between each group pair. Grey violins and boxplots represent the distribution of the distances obtained under the null model ($n = 9999$). Stars show significant differences between the observed value and the simulated ones.

Figure S2. Number of species into the four establishment levels for each Order (A) and families from the Cypriniforme order (B).

Figure S3. Date of first recorded introduction in an exotic location for 128 exotic fish species with record data along the levels of establishment (A) and adjusted p -values of associated post-hoc tests (B). The first record was retrieved from (Seebens et al., 2018) and we considered the minimal date of introduction in any region for each species (A). We then performed an Anova and post-hoc tests on 1000 resamples of the database with the same number of species ($n = 18$) for each group. Mean and standard deviation of adjusted p -values from the 1000 post-hoc tests are reported for each group

comparison (B). The group of super-established fish (More than 4 basins & Exists outside) slightly differed from the two groups of fish established in a smaller number of basins.

Figure S4. Proportion of exotic freshwater fish species having ecological impacts in each group along the levels of establishment. The four groups correspond to the establishment levels: species introduced inside their native bioregion in four basins or less ($\ln < 4$), inside their native bioregion in more than four basins ($\ln > 4$), outside their native bioregion in four basins or less ($\text{Out} < 4$), and outside their native bioregion in more than four basins ($\text{Out} > 4$). Groups showing significantly different proportions of species with impact are connected with red arrows. The Chi-squared tests and associated p -values are detailed in Table S4.

Figure S5. Basins and associated species richness of (A) the 547 exotic species contained in Tedesco et al. (2017) and (B) the 222 species with traits considered in this study. The basins that contained one of the 547 species but none of the 222 considered species are mapped in panel C. The richness (SR) is the total number of species either exotic or native contained in each basin for the considered pool ($n = 547$ or $n = 222$). The SR per basins is highly correlated between the two pools (Pearson's correlation coefficient = 0.96, $p < 0.001$).

Appendix 1. Material and methods used to link the establishment level with the ecological impact.

Appendix 2. Generalized linear models on the number of establishment basins: method and results.

Table S6. Variable importance and estimates (with their standard errors) of significant variables resulting from the GLM. The sign of the correlation depends on the category of reference for the variables Order and Parental Care. For the Order, the reference is the Acipenseriformes order. For the Parental Care the reference is the bearer category.

Figure S6. Number of basins of establishment for each considered fish species. The four species established in the highest number of basins are labeled and represented in red.

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