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Ecological and biological traits of non-native freshwater fish species differentiate them from native species in China

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ABSTRACT

China's freshwater ecosystems are gradually invaded by an increasing number of non-native fish species. However, to date, some controversy about the number of native and non-native freshwater fish species in wild habitats and very limited information on ecological or biological traits mediating fish introduction success at a national scale have prevented the proposal and implementation of targeted conservation and management strategies. To address these urgent issues, first we compiled an up-to-date inventory of 1,797 fish species (1,597, 84, and 116 native, exotic (originating from outside China), and translocated (originating from within China) species, respectively) along with 13 traits encompassing various ecological and life-history strategies for each species, which is the most comprehensive freshwater fish database in China as we know. Here, we found that non-native species mainly belonged to three orders (Perciformes, Siluriformes, and Cypriniformes) and three families (Cichlidae, Cyprinidae, and Salmonidae). Native species were significantly ($P < 0.001$) different from both exotic and translocated species according to their quantitative traits, while no remarkable differences between exotic and translocated species were detected ($P = 0.93$). Specifically, *G*-tests of independence, Similarity Percentage Analysis (SIMPER), and Mann-Whitney-Wilcoxon rank sum tests showed that compared to native species, species with relatively higher vulnerability (intrinsic vulnerability of fishes to fishing), trophic level, and pectoral fin vertical position, but less resilience and lateral body shape were deemed as potential candidates for introduction and dispersal in China.

1. Introduction

Over the past two hundred years, a considerable number of fish species have been intentionally or unintentionally introduced into novel regions across the globe, many of which established feral populations that inevitably exert effects on both aquatic ecosystems and economy in their recipient areas (Strauss et al., 2006; Gozlan, 2008; Cucherousset and Olden, 2011; Seebens et al., 2017). For instance, the most apparent effect of fish introductions to novel regions is changes in the composition of fish assemblages, which can cause taxonomic homogenization or differentiation (Toussaint et al., 2016a). Specifically, foreign exotic species tend to promote taxonomic differentiation (i.e., decrease in community similarity), while domestic translocated species normally exert a greater effect on taxonomic homogenization (i.e., increase in community similarity) (Leprieur et al., 2008; Toussaint et al., 2016a; Liu et al., 2017a).

With the increasing number of fish species introductions, fish invasions is becoming a more tricky environmental issue (Vitule et al., 2009; Gozlan et al., 2010) which poses a series of critical matters and challenges for fish conservation and management (Britton et al., 2011a; Britton et al., 2011b; Winfield et al., 2011). To develop and take effective conservation and management strategies aiming at minimizing dispersal and negative impacts of non-native species, mounting researches have been carried out to (a) identify species traits of successful invaders to monitor and reduce introductions of species with these traits or environmental characteristics (e.g., hydrology) of invaded habitats (e.g., Alcaraz et al., 2005; Vila-Gispert et al., 2005; Ribeiro et al., 2008; Su et al., 2020), (b) assess which species are more likely to become potential invaders affecting biodiversity (e.g., Moyle and Marchetti, 2006; Belmaker et al., 2013), and (c) predict potential invasive areas (e.g.,

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Fletcher et al., 2016). Among these studies, identifying species traits associated with fish introductions is receiving growing concern and paramount to help understand the ability of introduced species to spread and integrate themselves successfully into non-native regions (Marchetti et al., 2004; García-Berthou, 2007; Ribeiro et al., 2008; Belmaker et al., 2013). Many previous studies have evidenced that ecological or biological traits related to growth, reproduction, diet, food acquisition, or locomotion (Vila-Gispert et al., 2005; Toussaint et al., 2016b) could mediate non-native fish species establishment success (García-Berthou, 2007; Azzurro et al., 2014; Grabowska and Przybylski, 2015; Su et al., 2020). Nevertheless, ecological or biological traits involved in the success or failure of fish invasions from different regions are varied or even completely opposite due to various factors, such as distinct native fish faunas, invaders, studied geographical scales, ecosystem types, and socioeconomic activities (Vila-Gispert et al., 2005; Grabowska and Przybylski, 2015; Toussaint et al., 2018; Comte et al., 2021). Targeted researches on species traits of non-native species in particular regions are thus warranted.

Benefitting from diverse aquatic habitats and environments, China is one of the megadiverse countries containing high freshwater fish species richness (Xiong et al., 2015; Xing et al., 2016; He et al., 2020), but also providing suitable habitats for non-native fish species (Xiong et al., 2015). According to historical records, at least 439 non-native fish species were introduced in China (Xiong et al., 2015), representing the highest number of documented non-native fishes around the world, likely to put some of China's native fish species at high risk of extinction (Shuai et al., 2018; Zhang et al., 2018). For example, Liu et al. (2017a) demonstrated freshwater fish faunas homogenization across China resulted from species introductions and extirpations. With the increasing focus on the consequences of fish invasions in China, numerous related studies have been promoted in the past few years, such as testifying significant differences in functional attributes between native and non-native fish species in the Pearl River (Shuai et al., 2018) and evaluating current and future invasion risk of non-native freshwater fish species in China (Liu et al., 2019). Besides, several inventories of native and/or non-native freshwater fish species in China were also compiled (Kang et al., 2014; Xiong et al., 2015; Xing et al., 2016; Liu et al., 2017a; He et al., 2020). However, there is still some controversy about the number of native and non-native freshwater fish species in China's wild habitats, and our understanding of species traits involved in successful fish introductions at a national scale remains limited.

Here, our main objectives were to (a) compile an up-to-date inventory of native and non-native freshwater fish species in China's wild habitats along with the most comprehensive species trait database for these fishes through an extensive review of various sources, (b) explore whether the taxonomic distributions of native and non-native species differed significantly, and (c) test whether native and non-native species differed in their ecological or biological traits. We believe our compiled database could serve as a basis for further works and be useful for fishery scientists and resource managers to develop proactive strategies aiming at preventing more introductions of non-native species with traits related to fish introductions and ensuing fish invasions across China as well as in other countries.

2. Methods

2.1. Fish list

According to Kolar and Lodge (2001) and Xiong et al. (2015), a species introduced to areas beyond its native range is deemed as non-native species. Hence, we here defined two statuses for non-native freshwater fish species in China's wild habitats based on their definite distributional information provided by various resources: (a) exotic species are species introduced from other country or countries but not present originally in any basins in China and (b) translocated species are species native in one or more basins in China (e.g., common carp (*Cyprinus carpio*, Cyprinidae) and goldfish (*Carassius auratus*, Cyprinidae)) which had been introduced to other basin or basins in this country where they were not present originally. Moreover, native species are defined as species native in China which were not introduced to any other basins in this country according to related literature. Here, a comprehensive literature review, including about 800 peer-reviewed articles, monographs, various fish databases (e.g., FishBase and The Fish Database of Taiwan), official survey reports, and other sources, was conducted to obtain information on native, exotic, and translocated freshwater fishes in China. Species which spend a part of their life cycles (e.g., spawn and feed) in freshwaters were also included, but species with controversial status (e.g., mrigal carp (*Cirrhinus cirrhosus*, Cyprinidae) and *Acheilognathus tabira*, Cyprinidae) or occasionally occurring in freshwaters were excluded in our study. Most importantly, each species validity has been cross-checked and verified using FishBase (Froese and Pauly, 2019) and Eschmeyer's Catalog of Fishes (Fricke et al., 2020).

2.2. Species traits

Based on previous studies (e.g., Vila-Gispert et al., 2005; Ribeiro et al., 2008; Grabowska and Przybylski, 2015) and our expert' opinions, we collected 3 traits (i.e., resilience, trophic level, and vulnerability) that encompass various ecological and life-history strategies, such as growth, longevity, reproduction, diet, and mortality. What's more, morphological traits, determining fish roles in aquatic ecosystems (Toussaint et al., 2016b; Villéger et al., 2017) and evidenced to be related to fish introductions (Ribeiro et al., 2008; Su et al., 2020), were also selected.

One qualitative trait was taken into account: resilience (high, medium, low, and very low). Resilience obtained from FishBase means the minimum population doubling time of species estimated based on the rate (year^{-1}) at which the asymptotic length is approached (i.e., the von Bertalanffy Growth Function (VBGF) parameter *K*), fecundity, age at first maturity (t_m), or approximate maximum age of the population (t_{max}) (Froese et al., 2000; Froese et al., 2017; Froese and Pauly, 2019).

Twelve quantitative traits were taken into consideration as follows: trophic level, vulnerability, and 10 morphological traits mainly

Table 1
List of 10 morphological traits associated with food acquisition and locomotion (cited from Toussaint et al. (2016b) and Su et al. (2019) without modification).

Morphological traits	Formula	Potential link with fish functions	Reference
Maximum body length	*BLmax*	Size is linked to metabolism, trophic impacts, locomotion ability, nutrient cycling	e.g., Toussaint et al., 2016b; Froese and Pauly, 2019
Body elongation	$\frac{Bl}{Bd}$	Hydrodynamism	Reecht et al., 2013
Eye vertical position	$\frac{Eh}{Bd}$	Position of fish and/or of its prey in the water column	Winemiller, 1991
Relative eye size	$\frac{Ed}{Hd}$	Visual acuity	Boyle and Horn, 2006
Oral gape position	$\frac{Mo}{Bd}$	Feeding position in the water column	Dumay et al., 2004; Lefcheck et al., 2014
Relative maxillary length	$\frac{Jl}{Hd}$	Size of mouth and strength of jaw	Toussaint et al., 2016b
Body lateral shape	$\frac{Hd}{Bd}$	Hydrodynamism and head size	Toussaint et al., 2016b
Pectoral fin vertical position	$\frac{PFi}{Bd}$	Pectoral fin use for swimming	Dumay et al., 2004
Pectoral fin size	$\frac{PFl}{Bl}$	Pectoral fin use for swimming	Fulton et al., 2001
Caudal peduncle throttling	$\frac{CFd}{CPd}$	Caudal propulsion efficiency through reduction of drag	Webb, 1984

associated with food acquisition and locomotion of fishes (Table 1). Trophic level and vulnerability both taken from FishBase describe the rank of a species in a food web estimated based on diet information, food items or an ecosystem model, and intrinsic vulnerability of fishes to fishing estimated based on maximum length, t_m, VBGF parameter K, natural mortality rate, t_{max}, geographic range, fecundity or spatial behaviour strength, respectively (Froese et al., 2000; Cheung et al., 2005; Froese and Pauly, 2019). For maximum body lengths describing fish size taken from FishBase (Froese and Pauly, 2019), the unreasonable data (e.g., the maximum body length of one species provided by FishBase was found to be much shorter than its maximum total length) were removed or replaced by other appropriate records referring to the related literature. For the remaining morphological traits which are ratios of morphological measurements, 11 morphological measurements for each species (i.e., body length (*Bl*), body depth (*Bd*), head depth (*Hd*), caudal peduncle depth (*CPd*), caudal fin depth (*CFd*), eye diameter (*Ed*), eye position (*Eh*), oral gape position (*Mo*), maxillary jaw length (*Jl*), pectoral fin length (*PFl*), and pectoral fin position (*PFi*), Fig. 1) were measured on at least one scientific side-view drawing or good-quality picture of an entire adult animal collected from FishBase (Froese and Pauly, 2019), The Fish Database of Taiwan (Shao, 2020), Global Biodiversity Information Facility (GBIF; https://www.gbif.org/; retrieved in December 2020), and related literature using ImageJ software (https://imagej.nih.gov/ij/). For species with particular morphologies, several rules detailed in Toussaint et al. (2016b) and Su et al. (2019) have been adopted. For example, we only considered male morphology for species with sexual dimorphism due to the scarcity of female pictures for most species (e.g., Perciform and Cyprinodontiform species).

2.3. Statistical analysis

For possible missing traits in this study, an iterative imputation method, 'missForest', was adopted to fill the missing values among these traits (Stekhoven and Bühlmann, 2012; Penone et al., 2014). To test the efficiency of the random forest algorithm used to fill the missing values, the ratio of the number of possible missing values to the total number of actual and possible missing values was calculated and species along with complete values were extracted accordingly. Furthermore, actual values of the extracted values were randomly set as missing values according to the aforementioned ratio. A 'missForest' procedure was carried out to replace these missing values with simulated values and then these simulated values were compared to the actual values based on Spearman and/or Pearson correlation test.

For the qualitative variables (i.e., taxonomic order, family, and resilience), *G*-tests of independence (*G*-statistic) were applied to assess the association between the three species statuses and those aforementioned qualitative variables.

For the quantitative traits, a normalized principal component analysis (PCA) was applied (Abdi and Williams, 2010). The differences in PCA scores for native, exotic, and translocated species along the first two principal component (PC) axes were tested using one-way Analysis of Variance (ANOVA) with Tukey's *post hoc* tests. A Permutational Multivariate Analysis of Variance (PERMANOVA; 999 permutations) was also conducted, followed by multiple comparisons (Tukey's honestly significant difference test) to investigate the sources of variation in the quantitative traits among species status. When differences were detected, a Similarity Percentage Analysis (SIMPER) was applied to determine the individual contribution of each trait to the dissimilarity among species status after scaling the values for these quantitative traits by Min-Max normalization, with normalized values ranging from 0 to 1 (Clarke, 1993; Patro and Sahu, 2015). Finally, the nonparametric Mann-Whitney-Wilcoxon rank sum test was also chosen to test for each trait difference among species status (Wilcoxon, 1945; Mann and Whitney, 1947).

Likewise, the aforementioned analysis methods were also conducted for the subset of species without missing data (see Appendix B).

All statistical analyses were performed with R software version 3.5.2 (R Core Team, 2018) using the packages RVAideMemoire, missForest, factoextra, FactoMineR, pspearman, multcomp, and vegan.

3. Results

3.1. Taxonomic distributions

A total of 1,797 freshwater fish species belonging to 415 genera, 76 families, and 24 orders were recorded in China. The largest order was Cypriniformes (69.84%), followed by Perciformes (11.69%) and Siluriformes (10.91%). Moreover, the Cyprinidae (42.52%), Nemacheilidae (16.25%), and Gobiidae (5.73%) were the three most dominant families. Of the 1,797 fish species, 1,597 species, 61 families and 20 orders were native in China, 84 species, 23 families and 11 orders were exotic in at least one basin in China, and 116 species, 27 families and 12 orders were translocated in at least one basin in China, respectively. Among these species, taxonomic order and family frequencies significantly differed among species status (order: $G = 277.74$, d.f. $= 46$, $P < 0.001$; family: $G = 650.99$, d.f. $= 150$, $P < 0.001$). At the order level, the dominant orders of native, exotic, and translocated species were Cypriniformes (73.51%), Siluriformes (11.08%) and Perciformes (9.77%), Perciformes (42.86%), Siluriformes (14.29%) and Cypriniformes (10.71%), and Cypriniformes (62.07%), Perciformes (15.52%), Siluriformes (6.03%) and Osmeriformes (6.03%), respectively (Fig. 2). In addition, 3 and 1 of the 24 orders were only represented by exotic species (i.e., 3 lepisosteiform species, 4 characiform species, and 6 cyprinodontiform species) and translocated species (i.e., 1 gadiform species), respectively. At the family level, the dominant families of native, exotic, and translocated species

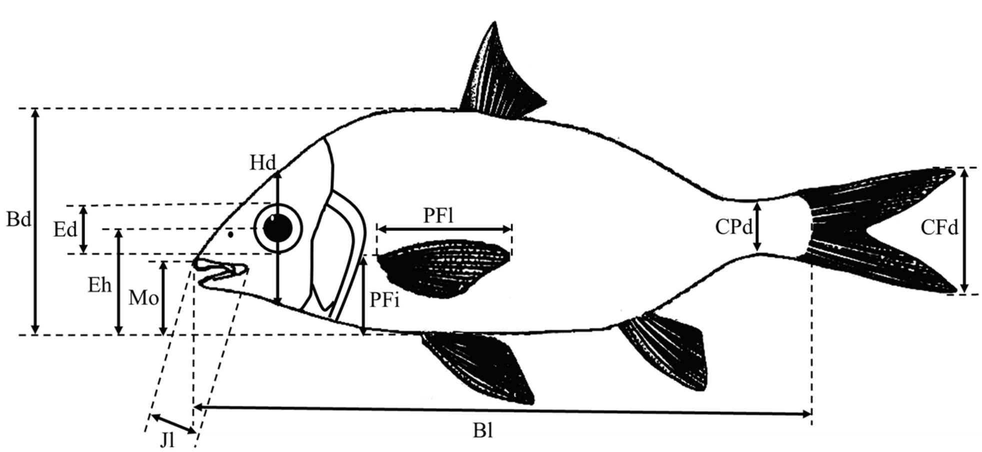

Fig. 1. The morphological measurements measured on each fish species. *Bl* body length, *Bd* maximum body depth, *Hd* head depth at the vertical of eye, *CPd* minimum depth of the caudal peduncle, *CFd* maximum depth of the caudal fin, *Ed* vertical diameter of the eye, *Eh* vertical distance between the centre of the eye to the bottom of the body, *Mo* vertical distance from the top of the mouth to the bottom of the body, *Jl* length from snout to the corner of the mouth, *PFl* length of the longest ray of the pectoral fin, *PFi* vertical distance between the upper insertion of the pectoral fin to the bottom of the body.

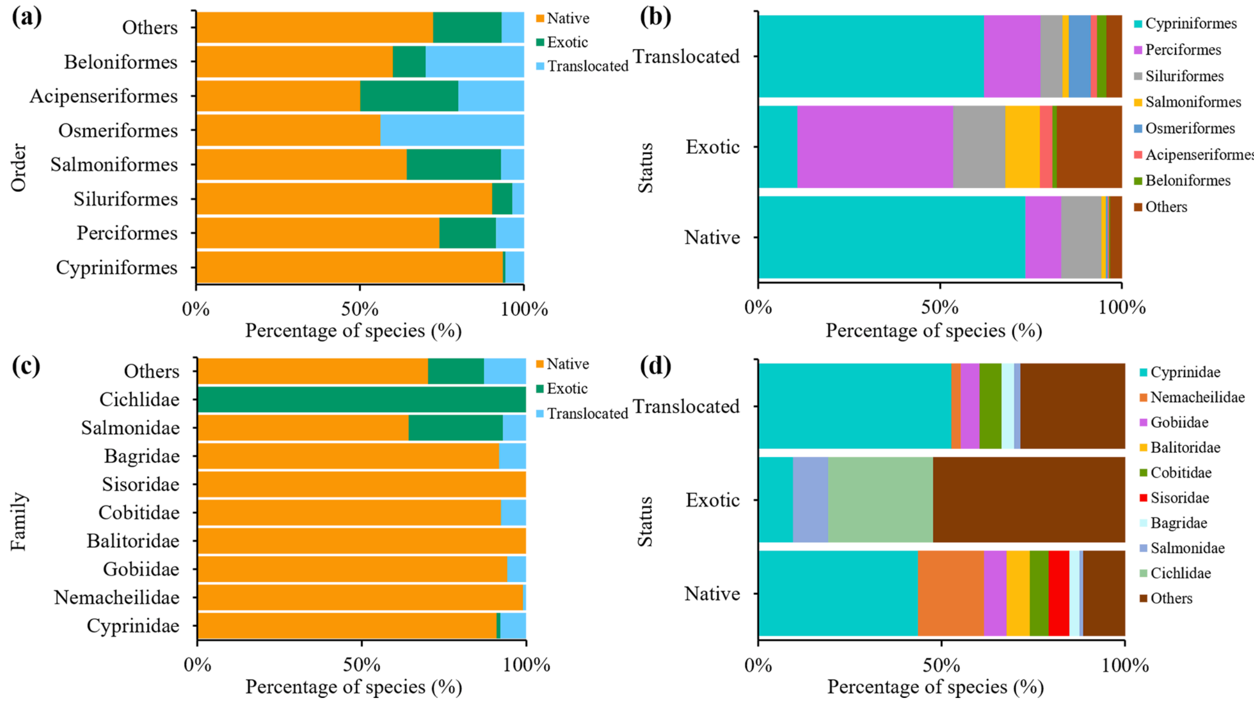

Fig. 2. (a) Percentages of the three species statuses in orders (only those with at least 10 species); (b) percentages of species in orders of each species status; (c) percentages of the three species statuses in families (only those with at least 20 species); (d) percentages of species in families of each species status.

were Cyprinidae (43.52%), Nemacheilidae (18.10%) and Balitoridae (6.32%), Cichlidae (28.57%), Cyprinidae (9.52%) and Salmonidae (9.52%), and Cyprinidae (52.59%), Cobitidae (6.03%) and Gobiidae (5.17%), respectively (Fig. 2). Besides, 10 and 4 of the 76 families were only represented by exotic species (i.e., 1 prochilodontid species, 1 osteoglossid species, 2 ambassid species, 3 serrasalmid species, 3 lepisosteid species, 3 ictalurid species, 5 loricariid species, 6 poeciliid species, 7 centrarchid species, and 24 cichlid species) and translocated species (i.e., 1 lateolabracid species, 1 latid species, 1 lotid species, and 1 plecoglossid species), respectively (see Appendix A: Table $A._1$).

3.2. Species traits

In total, 21,456 (91.85%) traits for 1,797 freshwater fish species including resilience, trophic level, vulnerability, and morphological traits were obtained in this study (Table 2). For the efficiency of the random forest algorithm used to fill the missing values, the Spearman's rho for the qualitative trait, resilience, was 0.88 and Pearson's r for the 12 quantitative traits ranged from 0.52 to 0.91 (Table 2), with an average of 0.75, indicating an overall good performance of the algorithm.

3.3. Analyses for the qualitative trait

Resilience frequencies significantly differed among the three species statuses ($G = 112.44$, d.f. $= 6$, $P < 0.001$). The majority (59.11%) of native species were found to have high resilience in contrast to 26.19% of exotic species and 21.55% of translocated species (Fig. 3). In addition, there were 7.58% of native species with low or very low resilience.

3.4. Analyses for the quantitative traits

The PERMANOVA test (see Appendix A: Table $A._2$) revealed significant traits differentiation among the three species statuses (PERMANOVA, $F = 80.17$, $P = 0.001$). Further multiple-comparisons (Tukey's HSD tests) showed that native species were significantly different from exotic species ($P < 0.001$) and translocated species ($P < 0.001$) for the

Table 2
Summary of data availability and efficiency of the random forest algorithm used to fill the missing values for the 13 traits (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$).

Species trait (Trait code)	Native (%)	Exotic (%)	Translocated (%)	Algorithm efficiency
Resilience (Res.)	86.91	95.24	100	0.88***
Trophic level (Tro. Level)	94.24	100	100	0.52***
Vulnerability (Vul.)	94.30	100	100	0.91***
Maximum body length (Max. Body Length)	93.55	98.81	100	0.80***
Relative eye size (Rel. Eye Size)	93.49	100	100	0.60***
Oral gape position (Oral Gape Pos.)	92.36	100	100	0.82***
Relative maxillary length (Rel. Maxil. Length)	73.07	97.62	92.24	0.72***
Eye vertical position (Eye Vert. Pos.)	91.67	100	100	0.82***
Body elongation (Body Elong.)	93.36	100	100	0.89***
Body lateral shape (Body Lat. Shape)	91.73	100	100	0.78***
Pectoral fin vertical position (Pec. Fin Vert. Pos.)	92.11	100	99.14	0.80***
Pectoral fin size(Pec. Fin Size)	92.36	98.81	100	0.62***
Caudal peduncle throttling (Cau. Ped. Throt.)	92.67	100	100	0.68***

12 quantitative traits, while no significant differences between exotic and translocated species were detected ($P = 0.93$). Consistent with the results from the PERMANOVA test, PCA scores of native species were significantly different from exotic and translocated species on both PC1 and PC2 axis, while no significant differences were observed between exotic and translocated species (Fig. 4). In addition, the first two PC axes

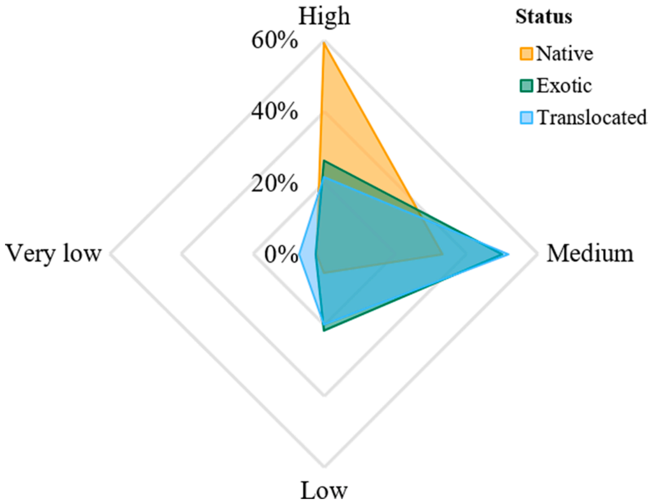

Fig. 3. Percentages of each resilience capacity (high, medium, low, and very low) within the different species statuses.

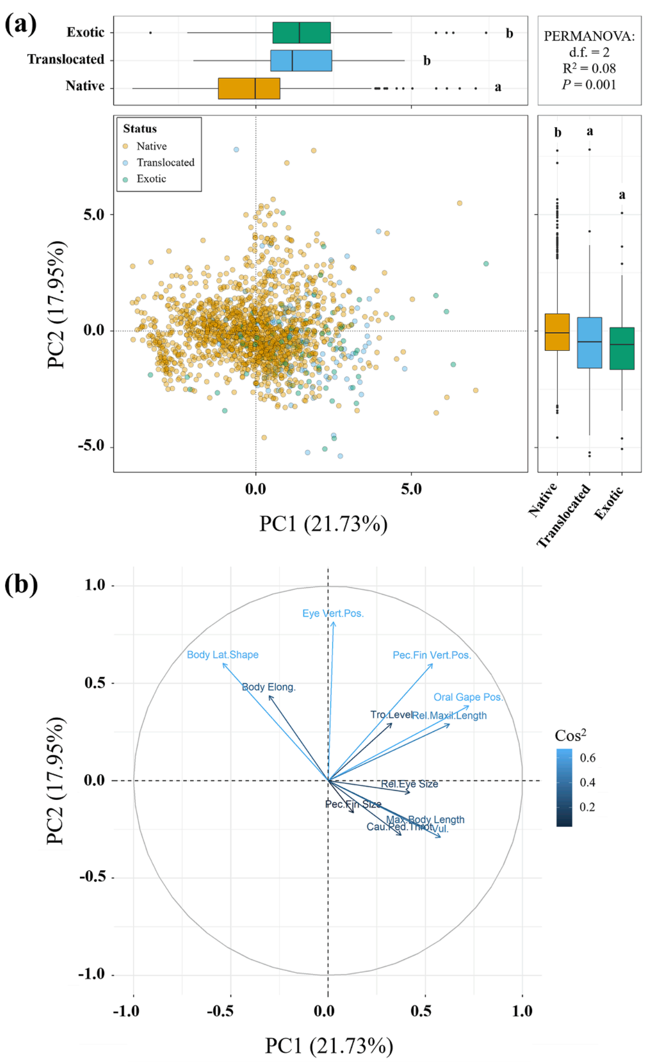

Fig. 4. Principal component analysis of the 12 quantitative traits for native, exotic, and translocated species in China: (a) species scores on the first two PC axes (different letters indicated significant differences); (b) correlation circle with squared cosine of the traits. Trait codes as in Table 2.

explained 39.68% of the total variance among the China's fish traits (see Appendix A: Table A.3). The PC1 axis mainly integrated oral gape position, relative maxillary length, and vulnerability (squared cosine of each trait ≥ 0.3). Species with higher positive values on PC1 were typically characterized as ferocious carnivorous species, e.g., some lepisosteid and silurid species while those with lower negative values were characterized as phytophagous or omnivorous species, e.g., some nemacheilid and balitorid species. The PC2 axis mainly integrated eye vertical position, body lateral shape, and pectoral fin vertical position (squared cosine of each trait ≥ 0.3). Species with higher positive values on PC2 were typically characterized as species with poor swimming ability inhabiting slow-flowing habitats, e.g., some gobiid species while those with lower negative values on PC2 were characterized as species with sustained or robust swimming ability inhabiting demersal habitats, e.g., some migratory species, acipenserid species.

The results of the Mann-Whitney-Wilcoxon rank sum tests of the 12 quantitative traits exhibited that native and exotic species as well as native and translocated species showed significant differences for 9 traits except relative eye size, eye vertical position, and relative maxillary length and for 11 traits except pectoral fin size, respectively (Table 3). The results of the SIMPER analyses demonstrated that the 12 quantitative traits differed in their contribution to the dissimilarity of native versus exotic species and native versus translocated species, respectively (Table 3). For these two groups, the cumulative contribution of the most shared discriminating species traits, vulnerability, trophic level, body lateral shape, and pectoral fin vertical position accounted for approximately 50% to the overall dissimilarities.

4. Discussion

In this study, 1,797 freshwater fish species in China were recorded accounting for over 10% of the total number of freshwater fish species across the world (Froese and Pauly, 2019), which is considerably greater than the numbers in any previous studies (e.g., 1,323 species in Xing et al., 2016 and 1,651 species in He et al., 2020) even though we adopted the same definition of freshwater fishes. Both the most comprehensive literature for collecting species and incorporating new species is speculated to be the key factors contributing to the highest species richness in the present study.

The increase of human activities, e.g., global trades and fishery activities, are generally accompanied by fish introductions (Xiong et al., 2015; Su et al., 2021). In China, the majority of exotic species were intentionally introduced for the purposes of trading, aquaculture, aquarium, and biocontrol (Xiong et al., 2015; Froese and Pauly, 2019). In contrast, except some translocated species with commercial or ecological importance intentionally introduced for human use, a significant proportion of them were inadvertently introduced. For instance, the introduction of *Rhinogobius cliffordpopei*, Gobiidae and *Rhinogobius giurinus*, Gobiidae, two small-bodied goby species with highly abundant populations in many lakes of China outside their natural ranges competing with native species for food resources (e.g., Guo et al., 2013), resulted from releasing other commercial fishes mingled with these two species (Du and Li, 2001). To date, a total of 200 non-native freshwater fish species (84 exotic species and 116 translocated species) were introduced and documented in wild habitats, which was the highest record of non-native fish species compared to previous studies and can represent the current situation of fish introductions in China's wilds to some extent (Xiong et al., 2015; Liu et al., 2017a). Our results suggested that the number of native, exotic, and translocated species by taxonomic order and family depended on their status. Exotic (23 families and 11 orders) and translocated (27 families and 12 orders) species belonged to relatively narrow spectrums of orders and families compared to native species (61 families and 20 orders), whereas translocated species belonged to a wider spectrum of orders and families than exotic species. Notably, like approximately 80% and 40% of non-native species in the other countries across the world just belonging to five orders

Table 3
The results of each quantitative trait difference between native and exotic species and native and translocated species tested by the Mann-Whitney-Wilcoxon rank sum tests and SIMPER summary of each trait contributing to the Bray-Curtis dissimilarity between these two groups (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

Trait	Native (average)	Exotic (average)	Translocated (average)	Native vs Exotic (% contribution)	Native vs Translocated (% contribution)
Vulnerability	28.43	42.39***	42.66***	14.29	15.75
Trophic level	3.01	3.13*	3.17***	14.07	12.35
Body lateral shape	0.58	0.52***	0.50***	10.20	11.43
Pectoral fin vertical position	0.27	0.31***	0.31**	10.01	10.57
Oral gape position	0.33	0.43***	0.44***	8.85	8.72
Relative eye size	0.32	0.33	0.39***	8.11	9.88
Pectoral fin size	0.17	0.20***	0.16	7.93	6.01
Caudal peduncle throttling	2.22	2.63***	2.52***	6.74	6.79
Body elongation	5.15	3.68***	4.76***	6.74	6.27
Eye vertical position	0.56	0.54	0.54*	5.34	6.03
Relative maxillary length	0.41	0.49	0.50***	4.23	3.41
Maximum body length	18.28	57.29***	43.87***	3.49	2.79

(Cypriniformes, Perciformes, Cyprinodontiformes, Siluriformes, and Salmoniformes) and three families (Cyprinidae, Cichlidae, and Salmonidae), respectively (Tedesco et al., 2017), Perciformes, Siluriformes, and Cypriniformes and Cichlidae, Cyprinidae, and Salmonidae were also dominant for China's non-native species. It seems that non-native species have tendencies to come from these orders or families. Besides, as pointed out by Moyle and Marchetti (2006), local familiarity with a taxon can contribute to spread of non-native species. In this study, even though 1 of the 24 orders and 4 of the 76 families were only represented by translocated species, all of them were historically already present in the ecosystem as native species, which may favour their spread. As for exotic species, 8 of the 20 native orders and 12 of the 61 native families contained both native and exotic species, conducive to their spread, but we found that there were 3 of the 24 orders and 10 of the 76 families only represented by exotic species. Hence, except for the most dominant taxa from exotic and translocated species, it's imperative to monitor the new record taxa in China as invaders were more likely to come from taxa that hadn't been already present in the native areas (Lockwood et al., 2001).

Generally, non-native species of interest for humans with various morphological traits mainly resulted from human selection or assistance (Su et al., 2020). Exotic species in China mostly selected by humans tended to have higher pectoral fin vertical position (swimming), but less lateral body shape (hydrodynamism) than native species, which indicated that considerable differences existed in their locomotion and habitat types. Intriguingly, although the purposes or ways of fish introductions between the majority of exotic and translocated species were distinct, we found that translocated species also possessed higher pectoral fin vertical position and less lateral body shape than native species, but were not considerably different from exotic species according to their morphology. Hence, not only purposes or ways of introduction dependent, the environmental filtering or biotic interactions should also be the probable explanations for the phenomenon (Kraft et al., 2015). Notably, corroborating the findings from many previous studies (e.g., Vila-Gispert et al., 2005; Toussaint et al., 2018; Su et al., 2020), exotic and translocated species in China were also found to have larger body size and less elongated body than native species but the fact was that maximum body length and body elongation only drove very few dissimilarities among the three species statuses (i.e., native vs exotic and native vs translocated). Namely, there's a more obvious trend for non-native species with higher pectoral fin vertical position and less lateral body shape to spread within China.

Trophic level was also a key trait distinguishing native and non-native species. Non-native species with different trophic levels, once introduced, might prey on or compete with native species for food resources, thereby inducing trophic niche shift in recipient areas (Britton et al., 2010; Correa et al., 2012). For example, some native species in Bosten Lake, China had been extinct due to the heavy predation effects of a translocated species, european perch (*Perca fluviatilis*, Percidae) (Xie and Chen, 1999). Besides, the composition of the fish fauna of Dianchi Lake, China obviously changed partly from feeding competition of massive populations of small-bodied non-native species, e.g., stone moroko (*Pseudorasbora parva*, Cyprinidae) and *Acheilognathus macropterus*, Cyprinidae (He and Liu, 1985). Beyond that, overfishing is another critical challenge to native species, as well as non-native species because almost all main water bodies in China were under heavy capture pressure (Zhao et al., 2015; Chen et al., 2020). Surprisingly, compared with exotic and translocated species, native species showed lower vulnerability (i.e., higher resilience), reflecting tendencies to have relatively smaller body size, lower age at first maturity, faster growth rate, higher natural mortality rate and fecundity, shorter potential longevity, or lower spatial behaviour strength (Froese et al., 2000; Cheung et al., 2005). Nonetheless, species with low vulnerability and/or high resilience would still face extinction risk considering threats from non-native species. As an example, the population of *Cyprinus chilia*, Cyprinidae, a native species with low vulnerability and high resilience used in the capture fishery, was on a declining trend in Dianchi Lake, China owing to their eggs fed on by non-native fish species during the spawning season (He and Liu, 1985). Additionally, it should also be noted that the minimum population doubling time for 7.58% of native species with low or very low resilience in China is as far as 4.5 years or more (Froese and Pauly, 2019), which may place them at the risk of extinction if they are confronted with long-term threats, such as the loss of spawning grounds and negative biotic interactions with non-native species (He and Liu, 1985; Du and Li, 2001; Guo et al., 2013; IUCN, 2021). Indeed, not each non-native species is likely to lead to adverse ecological effects, but could threaten native biodiversity if becoming invasive (Gozlan, 2008; Britton et al., 2011b). Thus, more seriously for native species is that some low vulnerable and/or high resilient exotic and translocated species with minor or no commercial importance exposed to less fishing pressure were found with high abundance in many lakes outside their natural ranges, e.g., *R. giurinus* and *Toxabramis swinhonis*, Cyprinidae (e.g., He and Liu, 1985; Ye et al., 2015), which seemed to confer competitive advantages to them in China's water bodies.

5. Conclusions

In conclusion, based on the largest number of freshwater fish species reported in China, this study evidenced that China's native species were significantly different from exotic and translocated species in their life-history traits and ecological species features which may provide abilities for non-native species to spread and establish populations or even replace native species in recipient areas (Liu et al., 2017b; Shuai et al., 2018). Since both exotic and translocated species differed from native species in their traits, further works are clearly needed to address how fish communities are affected by both introductions and translocations. Disentangling the effects of exotic and translocated species on community diversity (e.g., functional or phylogenetic) could be helpful to better understand how recipient communities have changed.

CRediT authorship contribution statement

Tao Xiang: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Software, Visualization, Writing - original draft, Writing - review & editing. **Xianghong Dong:** Conceptualization, Formal analysis, Investigation, Methodology, Software, Visualization, Writing - review & editing. **Gaël Grenouillet:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Methodology, Project administration, Resources, Supervision, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability statement

The data (e.g., the fish list and morphological data) that support the findings of this study are available from the corresponding author upon reasonable request.

Appendices. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2021.108218.

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