

Running Title: Native fish extinction risks from invasions

Phylogenetic relatedness predicts extinction risk of native freshwater fishes from non-native fishes across a latitudinal gradient

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Abstract

The strength of the inter-specific interactions between non-native and native species influence the subsequent invasion impacts, with stronger interactions and thus more severe impacts predicted when the species are phylogenetically close and co-exist at lower latitudes. Although work demonstrates non-native fish are more likely to invade areas which have phylogenetically closely related species present, the impacts of these invaders on the native species remain poorly understood. Accordingly, we conducted a comprehensive analysis of global freshwater fish occurrence data to test the phylogenetic niche conservatism hypothesis in co-occurring native and non-native freshwater fishes, assess whether non-native fishes drive extinctions of phylogenetically closely related native species, and evaluate how this varies with latitude. Phylogenetic niche conservatism was evident in co-occurring non-native and native fishes, with their morphometric trait dissimilarity significantly correlated with their phylogenetic distance. Extinct freshwater fishes were found to be more closely related to co-occurred non-native species than were species of other conservation statuses. However, the relationship between the extinction probability of native freshwater fishes and their phylogenetic relatedness to non-native species was context dependent, varying with latitude and across biogeographical realms. At higher latitudes, native fishes closely related to non-native species had a higher probability of extinction, whereas at lower latitudes, closely related native species were less likely to become extinct. Thus, the extinction risks posed by non-native fish vary spatially and depend

45 on their phylogenetic relatedness to native species, both of which are recommended for
46 consideration in invasion risk management programmes.

47

48 **Keywords**

49 Freshwater fish; extinction risk; biological invasion; phylogenetic relatedness; niche
50 similarity; latitude

1 INTRODUCTION

The consequences of non-native species for populations and communities of native species are strongly influenced by the strength of their inter-specific interactions, with impacts potentially including competitive displacement leading to population declines, extirpations and then even the extinction of native species (Gurevitch, & Padilla, 2004; Danet et al., 2024). Non-native species that are phylogenetic close to native species may share more resources and occupy similar niche with native species (Daehler, 2001), especially where the invader retains their niche-related traits from their native range (e.g. functional morphology) and so align to the niche conservatism hypothesis (Liu et al., 2020) and the phylogenetic niche conservatism hypothesis (Keppeler, & Winemiller, 2020; Losos, 2008). The phylogenetic relatedness and niche similarity between them likely result in intensified inter-specific competition (Daehler, 2001). Consequently, populations of co-existing native species that are most phylogenetically close to introduced non-native species could incur the most severe ecological impacts (Jackson et al., 2016; Britton et al., 2018).

The strength of inter-specific interactions between non-native and native species in freshwater ecosystems are often context dependent, being strongly influenced by the abiotic environment (Dodds et al., 2019). While non-native species that have traits that are well suited to the new environment (“pre-adapted”) are more likely to establish invasive populations, they are also likely to share traits with phylogenetically close

native species, increasing their biological interactions (Ricciardi, & Mottiar, 2006; Henriksson et al., 2015). The strength (and impacts) of these biotic interactions between non-native and native species are then predicted to be more intense at lower latitudes, where biodiversity tends to be more species rich (Schemske et al., 2009; Willig, Kaufman, & Stevens, 2003). At lower latitudes, the typically warmer and more stable climate—less prone to seasonal extremes than at higher, temperate latitudes—can lead to more diverse and abundant prey resources, which enhance species coexistence but could also intensify species interactions (Pastore et al., 2021; Dobzhansky, 1950; Willig et al., 2003). Consequently, the magnitude of non-native species' impacts on native species may vary across latitudinal gradients, resulting in spatially heterogeneous effects.

Freshwater ecosystems are undergoing substantial declines in their biodiversity, with approximately 25% of species now threatened with extinction (Sayer et al., 2025). While pollution, dams and water extraction, and land-use contribute significantly to these losses, biological invasions are increasingly recognized as a primary driver of extinction risk (Sayer et al., 2025; Bernery et al., 2022; Danet et al., 2024). Among non-native species, those phylogenetically closely related to native taxa are particularly potent predictors of local extinction risk (Pouteau, van Kleunen, & Strasberg, 2023; Bernery et al., 2022). Empirical data supporting this hypothesis in freshwater fishes is, however, absent, despite non-native fish being more likely to occur when closely related to native fishes, irrespective of their functional traits or niche similarity (Xu et al., 2022;

Xu et al., 2024). Building on the findings of Xu et al. (2024), who demonstrated that phylogenetically closely related non-native and native fishes are more likely to co-occur, we investigated whether such phylogenetic relatedness also contributed to increased extinction risk for native species. Specifically, we aimed to (i) assess the degree of phylogenetic niche conservatism in non-native and native freshwater fishes by examining the relationship between phylogenetic distance and the similarity in niche-related traits, (ii) investigate whether and how phylogenetic relatedness between co-occurring native and non-native species influences the extinction risks of native freshwater fishes, and (iii) evaluate how this relationship vary with latitude and across different biogeographical realms. Accordingly, the work should contribute to understandings of how non-native species influence native extinction risks and provide insights for biodiversity conservation and invasion risk management.

2 MATERIALS AND METHODS

2.1 Global freshwater fish occurrence and their phylogenetic relatedness

We used the global data of freshwater fish occurrence of Tedesco et al. (2017), which documents 14953 fish species inhabiting in 3119 drainage basins that together cover more than 80% of the Earth's surface. For each species occurrence, a native or non-native status was assigned in the dataset (Tedesco et al., 2017). Each drainage basin was provided with geographic information including the unique basin name, the country it

belongs, the corresponding biogeographic realm, and the centroid longitude and latitude coordinates (Tedesco et al., 2017).

Following Xu et al. (2024), we calculated two metrics to represent the phylogenetic relatedness between non-native and native species. Using the global phylogenetic tree for freshwater fish species from Xu et al. (2024), we calculated the phylogenetic distance between each pair of non-native and native species co-occurring within each drainage basin. For each native species, we then calculated the mean phylogenetic distance (MPD) to co-occurring non-native species, and the minimum near-neighbor phylogenetic distance to co-occurring non-native species, i.e. minimum near-neighbor taxa distance (MNTD).

2.2 Fish morphometric data

Morphological data for 8342 freshwater fish species—each characterized by ten functional and ecological niche-related traits—were obtained from the FISHMORPHO database (Brosse et al., 2021), a database for species inhabiting the six biogeographical realms of the globe. These morphometric data were used to construct a morphometric trait matrix for statistical analysis. By integrating these data with the global freshwater fish occurrence data (Tedesco et al., 2017) and the phylogenetic trees of Xu et al. (2024), a total of 8158 freshwater fish species were matched with both morphological traits and phylogenetic information. For these species, pairwise phylogenetic distances were calculated to analyze the relationship between morphometric trait and phylogeny.

2.3 Global freshwater fish conservation status

To quantify extinction risks for the native fishes, information on freshwater fish conservation status was extracted from the International Union for Conservation of Nature's (IUCN) of Threatened Species (hereafter 'IUCN Red List') in November, 2024 (Chamberlain, 2020; IUCN, 2024). Threatened species included those classified as near threatened (NT), vulnerable (VU), endangered (EN), critically endangered (CR), extinct in the wild (EW) and extinct (EX). The categories of EW and EX were merged into one category of extinct (EX). For those extinct species, their threats were extracted using the *redlist* R package (Chamberlain, 2020; IUCN, 2024).

2.4 Statistical analysis

The association between phylogeny and morphological traits were tested firstly by modeling a multivariate distance matrix regression between the morphological traits matrix and the phylogenetic distance matrix using the MDMR package (McArtor, 2018). Trait dissimilarity between species were calculated as the Gower distance (Gower, 1966) applied to the morphometric traits matrix. The association between trait dissimilarity and phylogenetic distance was examined using a mantel test by running the mantel function in the *vegan* package (Oksanen et al., 2022), with the correlation method of Pearson and 999 permutations. To examine phylogenetic niche conservatism between native and non-native freshwater fishes co-occurring within drainage basins, we modeled their trait dissimilarity as a function of phylogenetic distance using a

generalized linear mixed model (GLMM). The GLMM assumed a beta distribution with a logit link function and included a random effect of drainage basin nested in country and biogeographical realms (1|realm/country/basin).

To assess the impact of non-native fishes on the extinction risk of native freshwater species, we proceeded in two steps. First, we compared the density distribution of phylogenetic relatedness between non-native and native species (MPD and MNTD), and the centroid latitude of drainage basins inhabited with species, across conservation status categories of NT, VU, EN, CR, and EX. Next, we quantified native extinction probability binomially to distinguish extinct species from non-extinct taxa: extinct = 1 for EX; non-extinct = 0 for NT, VU, EN, CR. Native extinction probability was then modeled as a function of phylogenetic relatedness between native and non-native species (MPD or MNTD), the absolute value of the centroid latitude of the drainage basin, and their interaction. We fitted GLMMs in binomial distribution with clog-log link transformation as recommended for response variables with more zeros than ones (Zuur et al., 2009). The GLMMs were separately modeled for MPD and MNTD, with drainage basin nested in country and biogeographical realm (1|realm/country/basin) as a random factor for the global area. To analyze differences among different biogeographical realms and the global area, the GLMMs were also modeled for each biogeographical realm, initially specifying drainage basin nested in country (1/country/basin) as a random factor. If the variance component for either country or basin was estimated as zero, we simplified the random effects structure by dropping the

zero-variance terms. This simplification resulted in a random factor of basin (1|basin) for Nearctic and Australasia realms, a random factor of country (1|country) for Palearctic and Indo-Malay realms, and no random effects for Afrotropic realm. The stepwise approach preserves a maximal random structure and adheres to the principle of Barr et al. (2013). The GLMMs were executed using the *lme4* package (Bates et al., 2015). All GLMMs were assessed for dispersion adequacy using simulated residuals implemented in the *DHARMA* package (Hartig, 2022), with no significant evidence of either overdispersion or underdispersion detected ($P > 0.08$). For predictors exhibiting significant effects, we performed hierarchical variance partitioning through the *glmm.hp* package to quantify their relative contributions to the marginal variance (Lai et al., 2022). All statistical analysis were completed in R 4.4.1 (R Core Team, 2024).

3 RESULTS

3.1 Extinct freshwater fishes

Globally, 101 native freshwater fish species were assessed as extinct on the IUCN Red List. Threat information was available for 82 of these species, indicating that 45 extinctions were associated with the presence of non-native species (Table S1-S2). Phylogenetic relationships between the extinct and non-native species revealed that four of the extinct species were congeners with the corresponding non-native species, nine were in the same family and 10 were in the same order (Table S2).

The global data of freshwater fishes includes 56 extinct species (Table S1), reported across 75 drainage basins. The number of extinct species varied among drainage basins and biogeographical realms (Figure 1) with larger numbers in Nearctic realm (28) and Palearctic realm (12), and small numbers in Neotropic (9), Indo-Malay (6), Afrotropic (3) and Australasia (1) realms. Five extinct species were located in drainage basins without non-native species and thus were removed in analyzing their phylogenetic relationship with non-native species.

3.2 Phylogenetic niche conservatism in freshwater fishes

Each morphometric trait of freshwater fishes was associated significantly with the phylogenetic distance between species as suggested by the multivariate distance matrix regression (Table 1). When considering all morphometric traits together, the trait dissimilarity was significantly positively related with the phylogenetic distance as suggested by the Mantel test results (Mantel statistic r : 0.212, $P = 0.001$). For co-occurring native and non-native species, pairwise trait dissimilarity exhibited a significant positive relationship with their phylogenetic distance (Estimate = 0.361 ± 0.002 , $P < 0.001$, Table S3; Figure 2), indicating that phylogenetically closely related native and non-native species have greater similarity in morphometric traits.

3.3 Extinction risks of native fishes from non-native species

Phylogenetic relatedness metrics (MPD and MNTD) indicated that extinct fishes were generally more closely related to non-native species within their drainage basins than

were fishes in other conservation status categories (Figure 3). Moreover, native extinction probability varied significantly with the interaction of phylogenetic relatedness and geographical latitude (Figure 4; Table 2), with the interaction term of MPD $\times$ latitude and MNTD $\times$ latitude both showing strong significance ($P < 0.001$). These interaction terms have the highest individual marginal R^2 among predictors of the corresponding GLMMs for the global data (Table 2), indicating their highest importance in explaining the variation in native extinction probability. The GLMMs results suggested that the effect of phylogenetic relatedness between native and non-native species on native extinction risk was context-dependent and varied with latitude. At higher latitudes, native fishes close related to non-native species had a higher probability of extinction, whereas at lower latitudes, closely related native species were less likely to become extinct (Figure 4).

The GLMMs results also revealed distinct patterns among biogeographic realms (Figure 5; Table S4). In the Nearctic realm, the extinction probability of native species was significantly negatively associated with the phylogenetic relatedness between native and non-native species (MPD: $P < 0.05$; MNTD: $P < 0.01$; Table S4), while latitude had no significant effects on native extinction probability (Table S4), representing a high-latitude example consistent with the global pattern. The Palearctic realm demonstrated a similar pattern to the global trend, with a significant latitudinal gradient in the effects of the phylogenetic relatedness on the extinction probability (MPD $\times$ latitude: $P < 0.001$; MNTD $\times$ latitude: $P < 0.001$; Table S4). The Indo-Malay

realm also exhibited a latitudinal gradient in the effects of the phylogenetic relatedness on the extinction probability (MPD $\times$ latitude: $P < 0.01$, MNTD $\times$ latitude: $P < 0.05$; Table S4), but represent an example in low latitude area where high phylogenetic distance between native and non-native species contribute to high extinction risk (MPD: $P < 0.001$, MNTD: $P < 0.001$; Table S4). However, the Neotropical, Afrotropic or Australasia realms demonstrated no significant effects of the phylogenetic relatedness, latitude, or their interactions on the extinction probability of native freshwater fishes ($P > 0.1$ for all terms; Table S4).

4 DISCUSSION

This study aimed to identify whether phylogenetic niche conservatism exists between non-native and native freshwater fishes, quantify extinction risks to native fishes from invasions by phylogenetically closely related species, and evaluate how these risks vary with latitude and across biogeographical realms. The results supported the phylogenetic niche conservatism hypothesis in freshwater fishes with a significant association between niche-related trait dissimilarity and phylogenetic distances. There was a pattern evident where extinct native fish species exhibited close phylogenetic relatedness to co-occurring non-native fish, with this association varying significantly by latitude, showing greater strength at high latitude than at low latitude. The strength of the relationship between native extinction probability and phylogenetic relatedness to co-occurring non-native species also varied among biogeographical realms.

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271 Our findings demonstrate a significant positive correlation between morphometric trait
272 dissimilarity and phylogenetic distance between co-occurring native and non-native
273 freshwater fishes, coupled with significant associations between each morphometric
274 trait and phylogenetic distance. These results suggest that phylogenetically close related
275 non-native and native fishes share more similar functional traits, enabling them to
276 occupy similar ecological niches, thereby supporting phylogenetic niche conservatism
277 in non-native and native freshwater fishes. In combination with the niche conservatism
278 that ecological niches of species are conserved across space and time (Liu et al., 2020),
279 our findings indicate that closely related non-native and native freshwater fishes tend
280 to occupy similar ecological niches when they co-occur. Phylogenetic niche
281 conservatism has previously been a key assumption in hypothesis explaining
282 interactions between non-native and native species, such as the pre-adaptation
283 hypothesis (Darwin, 1859; Ricciardi, & Mottiar, 2006) and Darwin's naturalization
284 hypothesis (Daehler, 2001). Our study provides the first empirical support for
285 phylogenetic niche conservatism and its associated hypothesis in freshwater fish
286 species in global ranges.

287

288 Phylogenetic niche conservatism among non-native and native species implies the
289 importance of phylogenetic relatedness between them across all stages of biological
290 invasion, as it can influence both the abiotic adaptation of non-native species and their
291 competition with native species (Ricciardi, & Mottiar, 2006; Daehler, 2001). Our

findings demonstrate that the phylogenetic relatedness plays a significant role in the impact stage for freshwater fishes, building on the findings of Xu et al. (2024), who emphasized its importance in the establishment stage. In the establishment stage, non-native freshwater fish species closely related to native species are more likely to occur and establish (Xu et al., 2024), demonstrating a more pivotal role of adaptation to abiotic environments versus the outcomes of ecological processes such as inter-specific competition. In the impact stage, the established non-native fishes appeared to be involved in the extinction of closely related native fishes, especially at higher latitudes. This pattern suggests that close phylogenetic relatedness between established non-native and native species likely intensifies inter-specific competition among them, resulting in elevated extinction risks of native species particularly in harsh, seasonally variable environments at higher latitudes. Thus, the elevated extinction risk needs to be considered in invasion risk management strategies in regions where non-native and native fishes are phylogenetically close (Copp et al., 2016; Roy et al., 2018).

A latitudinal gradient was found in the extent to which closely related non-natives influence extinctions of native species, i.e. native species closely related to non-native species more likely become extinct at higher latitudes than at lower latitudes. The latitudinal gradient suggests a strong role of the abiotic environment in shaping how the impacts of biological invasions develop and progress. In the high latitude area, seasonal abiotic variability and extreme episodic events likely have strong influences on the high probability in the establishment of the non-native fishes closely related to native species

(Fan et al., 2023). The lower productivity and species richness of these systems likely result in restricted prey resources and lower resource breadth, increasing the strength of inter-specific competition between closely related non-native and native species (Pastore et al., 2021), potentially, the risk of population extirpation and ultimately species' extinctions (Smeti et al., 2018). The uneven distribution of extinct species across latitudes and among biogeographical realms, i.e. more extinct species at higher latitudes than at low latitudes, suggested that abiotic environment and resource breadth could have been influencing extinction risk more generally (Carscadden et al., 2020). In contrast, at lower latitudes, higher resource availability could drive the decrease in niche overlap and competition between closely related species (Pastore et al., 2021), facilitating biotic interactions between non-native and native species without triggering native extinctions (Fan et al., 2023). Moreover, limitations in conservation status assessments, particularly data scarcity, time-lags and methodological consistency (Butchart et al., 2025), likely contributed to the spatial heterogeneity in freshwater fish extinctions. This spatial heterogeneity suggested that environmental and anthropogenic stressors may interact with phylogenetic relationships between native and non-native species to determine the impact of biological invasions on native species. These findings highlighted the complexity of biological invasions and their consequences on biodiversity, underscoring the need for improving monitoring and data collection to accurately assess extinction risks, and management strategies that integrate environmental and anthropogenic stressors for effective conservation.

In summary, phylogenetic niche conservatism was evident in co-occurring native and non-native freshwater fishes in global ranges, providing empirical support for theories explaining invasion dynamics. Our results highlight the critical role of the phylogenetic relatedness between native and non-native species in determining invasion impacts. The phylogenetic relatedness was significantly influencing the extinction risk of native freshwater fish, with effects varying with latitudes, probably due to the intensified competition between close related non-native and native species in more harsh environments at high latitudes. The significance of the phylogenetic relatedness in both the establishment and impact stages underscored the importance of incorporating this factor into invasion risk and impact assessment processes, especially at high latitudes with harsh environments, for instance in the high latitude Palearctic and Nearctic realms of the northern hemisphere, where a large number of non-native fish species are now established (Tedesco et al., 2017; Xu et al., 2024).

AUTHOR CONTRIBUTIONS

Yingqiu Zhang: Conceptualization; formal analysis; methodology; funding acquisition; writing – original draft; writing – review and editing. **Yuefei Li:** Conceptualization; writing – review and editing. **Fangmin Shuai:** Conceptualization; writing – review and editing. **J. Robert Britton:** Conceptualization; writing – review and editing. **Jie Li:** Conceptualization; funding acquisition; writing – review and editing.

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COMPETING INTEREST

Each of the authors claims no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data and R code that support the findings of this study are available at <https://figshare.com/s/3ddf0136749426752b0a>. Original freshwater fish occurrence database is available at <https://doi.org/10.6084/m9.figshare.c.3739145.v1>. The phylogenetic tree for freshwater fishes is originally available at <https://doi.org/10.6084/m9.figshare.25058651>. FISHMORPH is originally available at <https://doi.org/10.6084/m9.figshare.14891412>. Fish conservation status is available at the IUCN Red List of Threatened Species (<https://www.iucnredlist.org>).

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FIGURE LEGENDS

FIGURE 1 Number of freshwater fishes classified as extinct (EX) or extinct in the wild (EW) in each drainage basin, based on the global freshwater fish occurrence data from Tedesco et al. (2017) and the IUCN red list.

FIGURE 2 Relationship between trait dissimilarity and phylogenetic distance in native and non-native species co-occurring within drainage basins

FIGURE 3 Density distributions of phylogenetic relatedness between co-occurring native and non-native freshwater fish species (a, mean phylogenetic distance (MPD); b, minimum near-neighbor taxa distance (MNTD)), and (c) the centroid latitude of the drainage basins inhabited with native species across the conservation status categories of near threatened (NT), vulnerable (VU), endangered (EN), critically endangered (CR), extinct in the wild (EW) and extinct (EX)

FIGURE 4 Latitudinal gradients in the relationship between the extinction probability of native freshwater fishes and their phylogenetic relatedness to non-native species in drainage basins. The phylogenetic relatedness was calculated as mean phylogenetic distance (MPD, a) and minimum near-neighbor taxa distance (MNTD, b) between native and non-native species. Line colors represent absolute latitude (0°-70°) of drainage basins.

FIGURE 5 Latitudinal gradients in the relationship between native extinction probability and the phylogenetic relatedness between native and non-native species within drainage basins of the Nearctic (a, d), Palearctic (b, e), and Indo-Malay (c, f) realms. The phylogenetic relatedness was calculated as mean phylogenetic distance (MPD) and minimum near-neighbor taxa distance (MNTD) between native and non-native species. Line colors represent absolute latitude (0°-70°) of drainage basins.

TABLES

Table 1 Conditional effects of each morphometric trait on phylogenetic distances

	Statistic	DF	Pseudo R ²	Analytic <i>P</i>
(All traits)	0.33091	10	0.24864	1e-20
MBI	0.00646	1	0.00485	1e-20
BEI	0.01239	1	0.00931	1e-20
VEp	0.01917	1	0.01440	1e-20
REs	0.00805	1	0.00604	1e-20
OGp	0.00908	1	0.00683	1e-20
RMI	0.00448	1	0.00337	1e-15
BLs	0.05005	1	0.03761	1e-20
PFv	0.15602	1	0.11723	1e-20
PFs	0.00875	1	0.00658	1e-20
CPt	0.00578	1	0.00434	1e-19

MBI: maximum body length; BEI: body elongation; VEp: vertical eye position; REs: relative eye size; OGp: oral gape position; RMI: relative maxillary length; BLs: body lateral shape; PFv: pectoral fin vertical position; PFs: pectoral fin size; CPt: caudal peduncle throttling. See detail definition for each morphometric trait in the FISHMORPH database (Brosse et al., 2021)

537 **Table 2** Dependence of native extinction probability on phylogenetic relatedness between native and non-native species (MPD and MNTD),
538 absolute latitude of drainage basins and their interactions, as indicated by coefficients of generalized linear mixed models. Variable importance
539 was assessed by hierarchical partitioning: unique marginal R^2 (Unique), average shared R^2 between predictors (Avg.share), individual marginal
540 R^2 (Individual) and individual contribution percentage (I.perc (%))

Predictor	Estimate	Std. Error	z value	Pr(> z)	Unique	Avg.share	Individual	I.perc (%)
~ MPD + latitude + MPD * latitude								
(Intercept)	-4.85	0.37	-13.18	0.000				
MPD	0.31	0.10	3.26	0.001	0.00130	-0.00040	0.00090	23.68
latitude	-0.06	0.25	-0.24	0.808	-0.00010	0.00020	0.00010	2.63
MPD:latitude	-0.43	0.11	-3.99	0.000	0.00320	-0.00040	0.00280	73.68
~ MNTD + latitude + MNTD * latitude								
(Intercept)	-5.06	0.42	-12.15	0.000				
MNTD	0.20	0.11	1.90	0.058	-0.00140	0.00090	-0.00050	-4.85
latitude	-0.16	0.26	-0.63	0.526	0.00100	-0.00020	0.00080	7.77
MNTD:latitude	-0.75	0.13	-5.68	0.000	0.01020	-0.00020	0.01000	97.09

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