Invasiveness reshapes the historical pattern of carp trait evolution

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Abstract

Human-mediated invasions are increasingly recognised as contemporary ecological disturbances with profound impacts on microevolutionary processes. However, whether such impacts extend beyond microevolutionary change to alter long-term evolutionary trajectories across lineages remains poorly explored. Using a global phylogenetic analysis of nearly 1,400 carp species (freshwater fishes of the family Cyprinidae), we show that invasiveness accelerates body size evolution more than twofold compared to native species, and it predictably redirects the macroevolutionary trajectories of key traits. Invasiveness has systematically directed species toward larger body sizes, greater range sizes, and cooler thermal niches. These results indicate that human-mediated introductions are a short-term force that can reshape the long-term, historical pattern of trait evolution. Invasions are not merely contemporary events, they are actively remodelling how species evolve in the Anthropocene, with important implications for anticipating future invasions under global change.

Introduction

Human activities are increasingly recognised as a dominant force shaping evolutionary processes across the planet. Many studies demonstrate that anthropogenic environmental change can drive rapid evolutionary responses within populations, altering trait distributions, genetic variation, and adaptive dynamics over contemporary timescales (1–3). These findings suggest that we are entering a novel evolutionary regime, the Anthropocene, in which human activity is affecting not only ecological systems but also the tempo and mode of evolution at global scales (4, 5). However, whether such impacts extend beyond microevolutionary change to alter long-term evolutionary trajectories across lineages remains unclear.

Biological invasions represent one of the most pervasive forms of human-mediated environmental change and provide a powerful framework for addressing its impact of long-term evolutionary change. Invasive species frequently experience strong and novel selection pressures associated with new environments, altered biotic interactions, and release from natural enemies (6–8). As a result, invasions are often accompanied by rapid evolutionary change in key traits, including life-history strategies, dispersal capacity, and environmental tolerances (9, 10). These shifts can occur over remarkably short timescales, sometimes within only a few decades following introduction (11, 12). Despite extensive evidence for such microevolutionary responses, it remains unresolved whether invasions systematically reshape evolutionary dynamics at macroevolutionary scales, including patterns of trait evolution across ancestor–descendant relationships.

Addressing this question is critical for understanding the extent to which invasions are deviating contemporary evolution from historical patterns. If human-mediated processes, such as invasions, bias the direction or rate of evolutionary change, they may fundamentally alter the structure of biodiversity and the distribution of traits across the tree of life (13). This has important implications for predicting species responses to global change, as evolutionary dynamics influence persistence, range expansion, and extinction risk under rapidly changing environments (14). Moreover, determining whether invasive species exhibit enhanced evolutionary potential may improve our ability to forecast future invasions, particularly under ongoing climate warming (15).

A key challenge in evaluating these ideas is the limited availability of fossil data for many clades which constrains direct comparisons between extant species and their common ancestors. Phylogenetic comparative approaches provide an alternative framework by leveraging information from extant species to infer evolutionary processes across both deep and contemporary timescales. This approach is particularly relevant for freshwater fishes such as the Cyprinidae, a diverse and globally distributed family with an evolutionary history extending back to the Eocene, exceeding ~50 million years (16, 17). Despite their ecological and evolutionary importance, the extent to which invasions have influenced their evolutionary trajectories remains poorly understood.

Here, we test whether human-mediated invasions have altered the evolutionary dynamics of cyprinid fishes using a global phylogenetic framework. By integrating species-level trait and distributional data with a comprehensive phylogeny, we quantify the direction and rate of evolutionary change in body size, life-history traits, geographic range size, and thermal niche across terminal phylogenetic branches. This approach allows us to measure evolutionary change from the most recent common ancestors to the extant native and invasive species, providing a comparative framework to test whether human-mediated invasions has reshaped the historical pattern of trait evolution.

If invasions reshape the macroevolutionary dynamics of Cyprinid fish, invasive species should exhibit consistent directional shifts in key traits relative to their most recent common ancestors, that is, across the phylogenetic terminal branches of invasive species. These trait-shifts are expected to differ significantly from those observed across the terminal branches of native species. Specifically, we predict that invasive species evolve towards larger body sizes, reflecting advantages in competition, dispersal, and predator avoidance (18–20). We further expect shifts towards life-history strategies characterized by higher fecundity and earlier maturation, consistent with a fast pace of life that facilitates rapid population growth during colonisation (6, 21, 22). Increases in population size may, in turn, enhance evolutionary potential, promoting expansion in geographic range and, therefore, we should observe directional shifts towards larger range size across terminal branches (23). Additionally, as extant invasive Cyprinids occupy colder habitats in comparison to native species (Supplementary Information), we predict directional shifts from warm-adapted ancestor towards cooler thermal niches in extant invasive species. Finally, we expect invasive species to exhibit elevated rates of evolutionary change across terminal branches due to strong and variable selection pressures in novel environments (10, 25, 26). By linking invasion success to macroevolutionary patterns of trait evolution, our study provides a test of whether human-mediated environmental change is reshaping the evolutionary trajectories of species across the tree of life.

Results

Trait evolution on the Cyprinid phylogeny. For all traits studied, the variable rate and variable rate regression model fitted the data better than the Brownian motion, Ornstein–Uhlenbeck, and Pagel's λ model, revealing substantial heterogeneity in evolutionary rates across the Cyprinidae phylogeny (Fig. 1a, Supplementary Fig. 1). Body size evolved dynamically, with accelerated rates in nearly half of the branches and fewer slowdowns (Fig 1a; Supplementary Table S1). Geographic range size showed the highest evolutionary lability, with over 50% of branches evolving at accelerated rates and no evidence of slowdowns (Supplementary Fig. 1, Supplementary Table 1). In contrast, life-history traits were more evolutionarily conserved. Fecundity and longevity evolved predominantly at constant rates, with some episodes of acceleration. Age at first maturity showed a distinct pattern, dominated by rate slowdowns (Supplementary Fig.1, Supplementary Table 1). The pattern of evolutionary rates remains qualitatively similar when rates were estimated by fitting the lambda-var-rate model, suggesting that measurement error may not be an important factor driving rate shifts across phylogenetic branches (see Methods). Overall, these results indicate that ecological traits related to spatial and morphological performance are more evolutionarily labile than life-history traits, providing a descriptive framework for assessing the influence of recent processes on trait evolutionary rates, such as the origin of human-induced invasion, across phylogenetic terminal branches.

Invasion has a positive effect on evolutionary rates. Using the terminal-branch evolutionary rates as a continuous response variable, we fitted phylogenetic generalized least square models, including invasive status as a binary predictor and estimating Pagel's λ to account for phylogenetic structuring in evolutionary rates. Results show that invasiveness has a significant effect on terminal-branch evolutionary rates for body size only (mean slope = 0.45, pMCMC = 98%). Body size evolved more than twice as fast in invasive species compared to native species (Fig. 1). Invasiveness did not affect the evolutionary rate of any of the other life history traits, range size, or temperature (Supplementary Table S2). Finally, all these results remain qualitatively similar when inferring rates by fitting the lambda-var-rate model, which indirectly accounts for unobserved error across traits (Methods).

Invasion differentially affects the direction of trait evolution. We fitted phylogenetic generalized mixed-effects regression models, predicting trait increase/decrease across terminal branches (binary response variable) by the invasive/native status (binary predictor variable) as fixed effect. We accounted for phylogenetic non-independence by including the phylogenetic variance-covariance matrix as random effect (see Methods). Results show that invasiveness significantly predicts higher probabilities of observing increases in body size (mean slope = 0.88, 95% CI: 0.52, 1.25) and geographic range size (mean slope = 1.24, 95% CI: 0.83, 1.67). On the probability scale, invasiveness has a 0.69% chance of body mass increase (Fig. 2a), and 0.74% chance of range size increase (Fig. 2b). On the other hand, invasiveness has a significant effect on the probabilities of observing directional changes in temperature but with lower probability for increases (mean slope = -0.41, 95% CI: -0.76, -0.06). On the probability scale, native species have a 53% chance of temperature increase which is significantly higher than 43% chance of temperature increase observed in invasive species (Fig. 2c). Finally, these results remain qualitatively similar when using the trait directions estimated from the lambda-var-rate model, which indirectly account for unobserved error across traits (Methods).

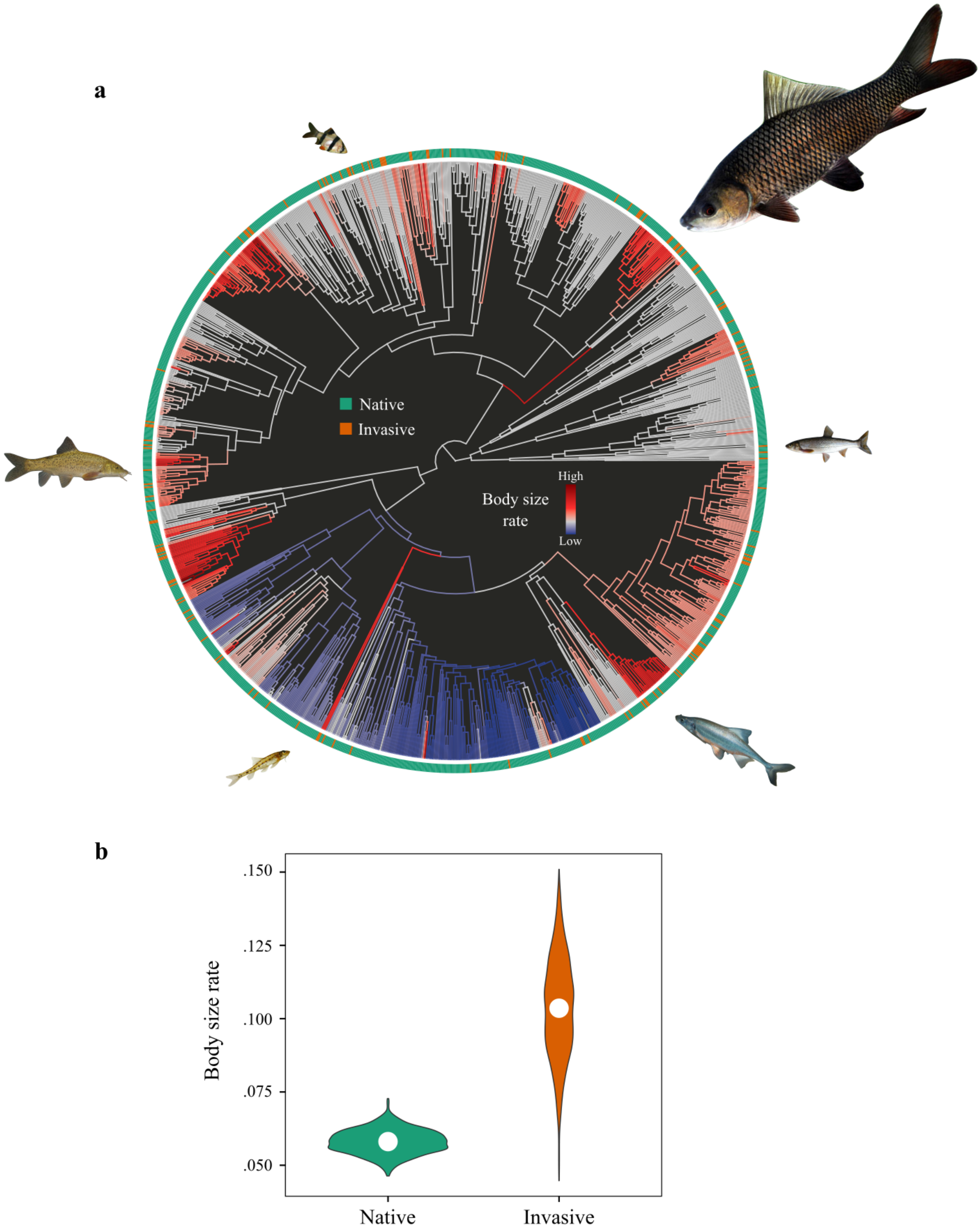

Figure 1. Invasive species accelerate the terminal-branch rate of body size evolution more than twofold compared to native species. (a) Phylogenetic tree of the Cyprinidae family with branches coloured according to the ($\log_{10}$) transformed median rate of body size evolution (high rates in red, low rates in blue, constant rate in grey). Branch rates were obtained by fitting the variable rate model in BayesTraits. **(b)** Predicted body size evolutionary rate ($\log_{10}$) across terminal phylogenetic branches for native (green) and invasive (orange) species.

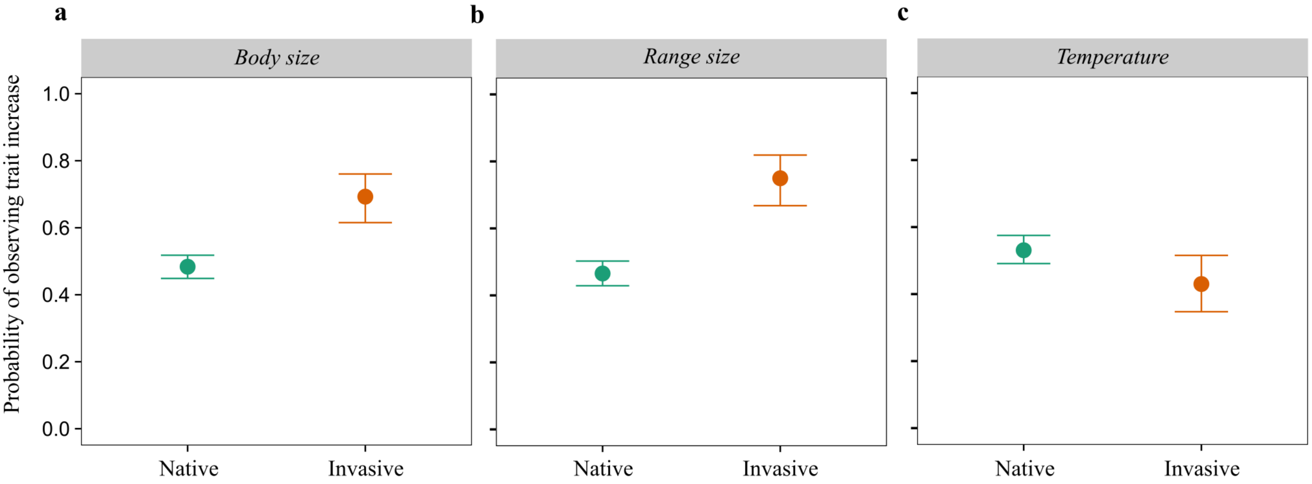

Figure 2. The probability of observing terminal-branch traits increases for native and invasive species. Plots show the results obtained from phylogenetic-mixed model fitting (Methods). Invasiveness (orange) has the highest probability of predicting increases in body size **(a)** and range size **(b)**. Temperature, on the other hand, is more likely to show increases in native (green) species **(c)**. Dots: mean probability; bars: 95% credible intervals.

Discussion

Human activities are reshaping evolutionary processes at unprecedented scales, but the macroevolutionary consequences of biological invasions, particularly whether they systematically reshape the historical patterns of trait evolution, have remained unresolved. Here, using a global phylogenetic comparative framework for the Cyprinidae family, we demonstrate that invasiveness acts as a powerful factor altering macroevolutionary change. Invasiveness significantly accelerated the rate of body size evolution across terminal branches and predictably biased the direction of trait evolution. Invasive lineages were more likely to evolve toward larger body sizes, larger geographic ranges, and cooler thermal niches, from their most recent ancestors. These shifts were absent for life-history traits (fecundity, longevity, age at maturity), whose evolutionary rates and directions remained unaffected. These findings provide direct phylogenetic evidence that human-mediated invasions are not merely ecological phenomena but active forces remodelling macroevolutionary patterns in the Anthropocene (27).

The accelerated rate of body size evolution in invasive cyprinids is particularly striking and aligns with the strong directional bias we observed toward increases in body size. Larger body size is a classic predictor of invasion success in fishes, conferring advantages in competitive dominance, dispersal capacity, predator avoidance, and resource acquisition in novel environments (28). Our terminal-branch analyses isolate the recent signal of human-mediated introductions, revealing that invasiveness imposes novel selection pressures capable of doubling the evolutionary rate of body size within the last few million years of evolutionary history. This result extends microevolutionary studies documenting rapid body size shifts in invasive populations to macroevolutionary scales (12, 29). Notably, the effect was specific to body size and not observed for life-history traits, despite these traits are highly correlated in Cyprinids. This result suggests that body size and life-history traits can evolved in an independent fashion in Cyprinids. Such decoupled pattern in the rate of trait evolution is consistent with broader independent phylogenetic evidence demonstrating that highly correlated traits (like physiological traits linked to endothermy) can evolve in a decoupled fashion over deep time (30).

Directional shifts toward larger geographic ranges further underscore the macroevolutionary signature of invasiveness. Range size is a strong proxy for environmental tolerance and adaptability, and larger ranges are commonly associated with invasion success across freshwater and marine taxa (31). Our finding that invasive species exhibit a 74% probability of range size increase on terminal branches implies that human introductions actively promote further expansion, likely through enhanced dispersal, enemy release, and population growth in recipient environments. By systematically favouring lineages capable of rapid range expansion, invasions may accelerate the global restructuring of freshwater fish faunas already documented under the Anthropocene (32).

The shift toward cooler thermal niches in invasive cyprinids is equally noteworthy and resolves an apparent paradox with microevolutionary expectations. Although many invasive fishes are assumed to track warming climates under current trends of warming, our data show that invasive species are disproportionately directed toward cooler realized thermal environments relative to their most recent common ancestors. This aligns with empirical observations of cyprinid invasions into temperate zones, where broad thermal tolerance and adaptation to cooler conditions facilitate establishment (33). Such niche shifts may arise from a combination of introduction bias, whereby translocations have historically concentrated cyprinid introductions in temperate freshwater systems used for aquaculture, stocking, and recreational fisheries, together with post-establishment processes such as local adaptation. Critically, the directional bias we detect on terminal branches suggests that invasions are not passively tracking contemporary climate but actively reshaping thermal niche evolution. This process implies that cooler-niche invaders may buffer against warming or, conversely, become vulnerable if temperate habitats warm beyond ancestral tolerances (34).

Recent conceptual work proposes that macroevolutionary metrics, including diversification rates, historical biogeographic dispersal, and rates of niche evolution, may help predict contemporary invasion potential (35). These metrics may capture intrinsic lineage properties such as niche breadth, dispersal capacity, and the ability to respond to novel environmental conditions, although the assumptions linking them to invasiveness remain largely untested (15). Under this framework, lineages with faster trait evolution may be more likely to establish and spread after introduction because they possess greater evolutionary flexibility. Consistent with this idea, the elevated evolutionary rates we detected in body size and geographic range suggests that rates of trait evolution could help identify lineages with latent invasion potential before invasions occur. More broadly, this perspective links deep-time evolutionary dynamics with invasion risk assessment, highlighting how evolutionary history may help prioritize taxa for monitoring under ongoing global change.

The lack of invasiveness effects on life-history trait rates or directions merits careful interpretation. Microevolutionary studies frequently report rapid shifts in fecundity, maturation, and longevity following invasion, driven by enemy release or novel resource availability (36). Our approach, however, reveals no such signal at the phylogenetic scale. Several non-mutually exclusive explanations may address these unexpected results. First, life-history traits may be more phylogenetically conserved in Cyprinidae, as evidenced by the predominance of rate slowdowns or constant rates in our variable-rate models. Strong historical constraints could limit recent redirection even under novel selection. Second, data limitations (e.g., fecundity available for only 444 species) could reduce power for these traits relative to body size (1,241 species). Regardless, this contrast highlights that not all “invasive traits” manifest equivalently at micro versus macroevolutionary scales, reinforcing the value of phylogenetic approaches for distinguishing contemporary adaptation from deeper evolutionary patterns (37).

Our results contain important caveats. The classification of invasiveness (158 invasive vs. 1,210 native species) follows standard criteria but may conflate transport, establishment, and spread stages. Finer resolution, for example, considering residence time or invasion stage, could reveal additional insights. Trait datasets, while comprehensive, are incomplete for life-history variables and rely on maximum reported values that may incorporate measurement error, but our lambda-variable-rate models explicitly mitigated this bias. The Fish Tree of Life phylogeny is the most taxonomically complete available, but unsampled diversity or topological uncertainty could influence rate estimations and ancestral state reconstructions. Finally, human stocking practices may introduce non-random bias toward larger-bodied or fast-growing lineages, potentially amplifying the observed patterns. Nonetheless, the consistency of results across rate (using BayesTraits) and directional (using brms phylogenetic GLMMs) analyses, and their robustness to error correction, supports the robustness of the core findings.

Taking together, these patterns position biological invasions as a short-term but powerful force capable of reshaping long-term evolutionary trajectories. By accelerating body size evolution and redirecting lineages toward larger sizes, broader ranges, and cooler niches, human-mediated introductions are superimposing a novel macroevolutionary signature onto the Cyprinidae tree of life. More broadly, our study contributes to emerging evidence that the Anthropocene is defined not only by extinction and homogenization but by active human-driven redirection of macroevolution (38, 39). Extending these phylogenetic comparative approaches to other clades, integrating fossil calibrations where available, and modelling interactive effects of invasions with climate change will further illuminate how humanity is rewriting the evolutionary rules of the biosphere.

Methods

To test the hypotheses that invasions reshape evolutionary patterns, we modelled the evolutionary rate and direction of six Cyprinid traits: body size, fecundity, longevity, age at maturity, geographic range, and environmental temperature; estimating both evolutionary parameters across the branches of the Cyprinid phylogenetic tree. We then tested if the presence of invasiveness affected trait evolutionary rate and direction of change on terminal branches of the Cyprinid tree. We tested the effect of invasiveness on evolutionary patterns across terminal branches because the presence of human-mediated invasions appeared in recent times, long after the last speciation events that gave rise to the extant diversity of Cyprinid fishes. Therefore, any potential effect of invasions on trait evolutionary rate and direction of change will be reflected only in the terminal branches of the phylogenetic tree that link extant species to their most recent common ancestor.

Study model. To test hypotheses, we used fish species of the family Cyprinidae. They are one of the most widely introduced fish families, comprising about 2,950 species. They document introductions dating back to the 17th century (40, 41), often for aquaculture, ornamental, or consumption purposes (42–44). The common carp (*Cyprinus carpio*), for instance, is considered the first domesticated fish, cultivated by the Romans nearly 2000 years ago (45). Their broad phylogenetic diversity and variation in life-history traits make them ideal for evaluating how invasiveness shapes evolutionary dynamics.

Phylogenetic tree. We obtained a calibrated phylogeny of Cyprinidae from The Fish Tree of Life (17) (https://fishtreeoflife.org/), which contains 1,368 species (Supplementary Dataset 1). We used this phylogeny because it is the most taxonomically complete phylogeny available for Cyprinidae to date. Its broad species coverage and standardized reconstruction make it the current reference framework for comparative analyses in freshwater fishes.

Species' trait data. To assess whether the ecological process of species introduction predicts systematic changes in the rate of trait evolution, we compiled a comprehensive trait dataset for Cyprinids fish species. Body size was recorded as the maximum reported total length (in centimetres), with available data for 1,241 species (Supplementary Dataset 2). Reproductive rate was measured as maximum absolute fecundity and was available for 444 species (Supplementary Dataset 2). Longevity was defined as the maximum recorded lifespan, with data for 249 species (Supplementary Dataset 2). Age at first maturity was included for 363 species based on available life-history records Supplementary Dataset 2). Trait data were sourced from FishBase (46); fishbase.org, and complemented, when necessary, with additional information extracted from diverse primary literature sources.

Species' geographic data. We quantified geographic range size as the Extent of Occurrence (EOO) area (in square kilometres), representing the minimum area encompassing all known occurrence records of each species. A species' geographic range is considered a strong indicator of its environmental adaptability (47) and environmental tolerance (48). Species with broader ranges can persist across diverse conditions, which enhances their survival and spread in novel habitats (49). Therefore, this metric is frequently used as a predictor for successful establishment (48) and introduction success (50) in both freshwater (49) and marine species (47, 48). Distribution data were obtained for 1,155 species from the Global Biodiversity Information Facility (GBIF; gbif.org) and the International Union for Conservation of Nature (IUCN; iucnredlist.org) (Supplementary Dataset 2). Occurrence records were filtered using the platform's quality controls, excluding records with spatial issues (e.g., invalid coordinates, zero coordinates, and freshwater species plotted in marine environments). Additional erroneous points were removed through manual inspection to correct georeferencing errors. This filtering ensured that only spatially reliable records were retained for estimating species' geographic ranges.

Species' environmental data. In this study, we define "environmental conditions" as the thermal regime experienced across each species' distribution range, quantified as annual average temperature. In addition, the latitudinal range was used as a proxy for the breadth of environmental tolerance and climatic niche space. Values were extracted for 1,081 species using the EarthEnv database (51) (earthenv.org) (Supplementary Dataset 2), which provides global-scale climate data for freshwater ecosystems at a 1 km resolution. We used the stream-surface annual average temperature as our environmental variable. For each species, we calculated the mean temperature across its distribution range using the "Zonal Statistics" tool in QGIS (QGIS Development Team, 2020), based on polygonal species occurrence data. This value reflects the integrated thermal environment experienced by populations throughout the species' latitudinal range.

Species invasion status. Species were classified as invasive when there was documented evidence of established populations outside their native range, otherwise they were identified as native. This criterion follows widely accepted definitions in invasion biology (52–54). We obtained a subset of 158 invasive and 1210 native species within the database, based on information compiled from FishBase (46) (fishbase.org) and the Global Invasive Species Database (GISD; iucngisd.org).

Trait evolutionary rates across phylogenetic branches. To assess whether invasive species show a distinct pattern in evolutionary rates of body size, we employed the variable rate model in BayesTraits v5.0.3 (55). This phylogenetic model adjusts phylogenetic branch lengths to accommodate areas of the tree where the inferred variance in trait evolution (or amount of evolutionary change) of the trait exceeds or falls below the expected background Brownian model (BM) rate. The rate of phenotypic change occurring in the branches is divided into two components: a constant rate parameter (σ^2_b) and a set of branch scalars (r) that identify branch-specific deviations from the background rate by adjusting branch lengths, obtaining an optimized variance for each branch. Stretching or compressing a branch is like increasing or decreasing the rate of phenotypic change relative to the rates of an underlying time-proportional Brownian change process.

To estimate evolutionary rates of traits that correlate with body size, such as longevity, geographic range, reproductive rate, and age at first early maturity, we employed the variable rate (VR) phylogenetic regression model in BayesTraits v 5.0.3 (56, 57). This method is an extension of the variable rate model, and it is designed to assess the overall relationship between a trait of interest (e.g., longevity as the response variable) and other traits (e.g., body size as the predictor) and to detect shifts in the evolutionary rate of the residual variance of the regression.

Inference of the magnitude of the r-scalars per branch was evaluated in a Bayesian framework with Markov chains and Monte Carlo (MCMC) and reversible jump, generating the posterior distribution of trees with scaled branch lengths. MCMC was generated for 200 million iterations, with sampling every 50,000 iterations to ensure independence in model parameters. Models postprocess and estimation of median r values were conducted in R-package BayesTraitR (57) (https://github.com/joannabaker/BayesTraitR).

Accounting for trait error in branch-rate estimation. Trait error introduces systematic biases in the estimation of key model parameters, often leading to underestimation of phylogenetic signal and overestimation of evolutionary rates or selection strengths (58, 59). Because we lack information on the error associated with the traits used in this study, we employed an alternative approach to indirectly account for unobserved error across traits when estimating branch-specific evolutionary rates. Specifically, unobserved error adds independent noise to tip values, which reduces observed covariances among related species and thereby diminishes the apparent phylogenetic signal of traits. Thus, Pagel's λ can absorb some of this error by downscaling the phylogenetic structure, improving model fit without explicit error terms. We therefore fitted a lambda-var-rate model in BayesTraits v5.0.3, which estimates Pagel's λ followed by the estimation of r scalars in each MCMC iteration. As a result, evolutionary rates across phylogenetic branches are estimated on top of the tree with branches scaled by the λ parameter.

Invasion effect on evolutionary rates across terminal branches. We conducted phylogenetic ANOVAs to test whether rates of evolutionary change along terminal branches differ between invasive and non-invasive species. Specifically, we fitted a phylogenetic regression in which the response variable was the rate of change estimated for each terminal branch, calculated as the median r-scalar from the posterior Bayesian distribution of branch-specific rates. Invasive status (invasive = 1, native = 0) was included as a binary explanatory variable. We estimated the Pagel's λ parameter, as evolutionary rates across terminal branches of the tree might correlate with the structure of the phylogeny, i.e., terminal branch rates might show significant phylogenetic signal (60). To account for the potential biases associated with unobserved trait error, we fitted all the phylogenetic ANOVAs using the evolutionary rates estimated from the lambda-var-rate model fit.

Phylogenetic ANOVAs were performed in BayesTraits v5.0.3. MCMC chains were generated with 200 million iterations, sampling every 50,000 iterations. Regression coefficients were considered significant according to a calculated pMCMC value. The estimated parameter is considered significant if its value is greater or less than zero by more than 95% of iterations.

Invasion effect on directional changes across terminal branches. We obtained the evolutionary direction across terminal branches for six traits: body size, geographic range, fecundity, longevity, age at first maturity, and environmental temperature. For this, we first estimated ancestral states at phylogenetic nodes, using the trees with scaled branches according to the median rate of trait evolution as obtained from the variable rate model. Ancestral states were inferred using the *ace* function of the *ape* R-package (61). We assumed a constant rate, Brownian motion model to reconstruct ancestral states. However, we used the median scaled tree obtained from the variable rate model, so that we can incorporate variation in the rate of evolution when estimating ancestral states at each node in the phylogeny (62).

Having estimated ancestral states for each of the six traits, we classified changes across terminal branches. We treated these changes as a binary variable, representing increases or decreases from the inferred values at the most recent internal nodes. We then tested for differences in trait evolutionary direction between invasive and native species by fitting six separate Bayesian phylogenetic generalized mixed-effects models in the *brms* R-package (version 4.0) (63). Each model treated the binary response variable, indicating trait increase (1) or decrease (0) as the outcome, modelled under a Bernoulli distribution with a logit link function to estimate probabilities of trait increases. Species status (invasive = 1, native = 0) was included as a fixed-effect predictor to assess its directional influence on the probability of trait increase. To account for phylogenetic non-independence among species, we incorporated a random intercept grouped by species, with the covariance structure informed by a phylogenetic correlation matrix derived from the group's ultrametric tree. Models were estimated using Hamiltonian Monte Carlo sampling with four chains, 2,000 iterations (1,000 warm-up), and weakly informative priors normal (0,1) for intercepts and coefficients, and exponential (1) for standard deviations. Model convergence was verified via R-hat values (<1.01) and effective sample sizes (>400), with posterior predictive checks confirming adequate fit. We identified the fixed effect (invasive) as significant when the 95% credible intervals for the estimated slope on the logit scale excluded zero. Finally, to account for the potential biases associated with the unobserved trait error, we fitted all the phylogenetic mixed models using the direction of trait evolution estimated from the lambda-var-rate model fit.

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References

1. S. R. Palumbi, Humans as the world's greatest evolutionary force. Science 293, 1786–1790 (2001).
2. S. P. Carroll, A. P. Hendry, D. N. Reznick, C. W. Fox, Evolution on ecological time-scales. Functional Ecology 21, 387–393 (2007).
3. M. Alberti, et al., Global urban signatures of phenotypic change in animal and plant populations. Proceedings of the National Academy of Sciences 114, 8951–8956 (2017).
4. S. P. Otto, Adaptation, speciation and extinction in the Anthropocene. Proc Biol Sci 285, 20182047 (2018).
5. F. Pelletier, D. W. Coltman, Will human influences on evolutionary dynamics in the wild pervade the Anthropocene? BMC Biol 16, 7 (2018).
6. A. K. Sakai, et al., The Population Biology of Invasive Species. Annual Review of Ecology, Evolution, and Systematics 32, 305–332 (2001).
7. H. A. Mooney, E. E. Cleland, The evolutionary impact of invasive species. Proceedings of the National Academy of Sciences 98, 5446–5451 (2001).
8. K. D. Whitney, C. A. Gabler, Rapid evolution in introduced species, 'invasive traits' and recipient communities: challenges for predicting invasive potential. Diversity and Distributions 14, 569–580 (2008).
9. R. I. Colautti, J. A. Lau, Contemporary evolution during invasion: evidence for differentiation, natural selection, and local adaptation. Mol Ecol 24, 1999–2017 (2015).
10. P. J. Prentis, J. R. U. Wilson, E. E. Dormontt, D. M. Richardson, A. J. Lowe, Adaptive evolution in invasive species. Trends Plant Sci 13, 288–294 (2008).
11. C. E. Lee, Evolutionary genetics of invasive species. Trends in Ecology & Evolution 17, 386–391 (2002).
12. K. A. Hodgins, D. G. Bock, L. H. Rieseberg, "Trait Evolution in Invasive Species" in Annual Plant Reviews Online, (John Wiley & Sons, Ltd, 2018), pp. 459–496.
13. A. P. Sullivan, D. W. Bird, G. H. Perry, Human behaviour as a long-term ecological driver of non-human evolution. Nat Ecol Evol 1, 65 (2017).
14. M. C. Urban, et al., Improving the forecast for biodiversity under climate change. Science 353, aad8466 (2016).
15. S.-S. Weil, M. Habrant, S. Lavergne, W. L. Allen, L. Gallien, Can macroevolution inform contemporary invasion potential? Biol Invasions 27, 199 (2025).
16. T. M. Cavender, "The fossil record of the Cyprinidae" in Cyprinid Fishes: Systematics, Biology and Exploitation, I. J. Winfield, J. S. Nelson, Eds. (Springer Netherlands, 1991), pp. 34–54.
17. D. L. Rabosky, et al., An inverse latitudinal gradient in speciation rate for marine fishes. Nature 559, 392–395 (2018).
18. B. L. Phillips, G. P. Brown, R. Shine, Evolutionarily accelerated invasions: the rate of dispersal evolves upwards during the range advance of cane toads. Journal of Evolutionary Biology 23, 2595–2601 (2010).

19. B. L. Phillips, G. P. Brown, J. K. Webb, R. Shine, Invasion and the evolution of speed in toads. Nature 439, 803–803 (2006).
20. R. Shine, G. P. Brown, B. L. Phillips, An evolutionary process that assembles phenotypes through space rather than through time. Proceedings of the National Academy of Sciences 108, 5708–5711 (2011).
21. S. L. Pimm, The Balance of Nature?: Ecological Issues in the Conservation of Species and Communities (University of Chicago Press, 1992).
22. M. Rejmanek, D. M. Richardson, What Attributes Make Some Plant Species More Invasive? Ecology 77, 1655–1661 (1996).
23. D. Houle, D. M. Rossoni, Complexity, Evolvability, and the Process of Adaptation. Annual Review of Ecology, Evolution, and Systematics 53, 137–159 (2022).
24. C. Liu, C. Wolter, W. Xian, J. M. Jeschke, Most invasive species largely conserve their climatic niche. Proceedings of the National Academy of Sciences 117, 23643–23651 (2020).
25. B. M. Ochocki, T. E. X. Miller, Rapid evolution of dispersal ability makes biological invasions faster and more variable. Nat Commun 8, 14315 (2017).
26. W. Gong, et al., The rapid evolution of an invasive plant due to increased selection pressures throughout its invasive history. Ecotoxicol Environ Saf 233, 113322 (2022).
27. M. Baltazar-Soares, K. I. Brans, C. Eizaguirre, Human-induced evolution: Signatures, processes and mechanisms underneath anthropogenic footprints on natural systems. Evol Appl 14, 2335–2341 (2021).
28. E. García-Berthou, The characteristics of invasive fishes: what has been learned so far? Journal of Fish Biology 71, 33–55 (2007).
29. K. D. Whitney, C. A. Gabler, Rapid evolution in introduced species, ‘invasive traits’ and recipient communities: challenges for predicting invasive potential. Diversity and Distributions 14, 569–580 (2008).
30. J. Avaria-Llautureo, C. E. Hernández, E. Rodríguez-Serrano, C. Venditti, The decoupled nature of basal metabolic rate and body temperature in endotherm evolution. Nature 572, 651–654 (2019).
31. B. H. Daru, et al., Widespread homogenization of plant communities in the Anthropocene. Nat Commun 12, 6983 (2021).
32. B. H. Daru, et al., Widespread homogenization of plant communities in the Anthropocene. Nat Commun 12, 6983 (2021).
33. A. Ruiz-Navarro, P. K. Gillingham, J. R. Britton, Shifts in the climate space of temperate cyprinid fishes due to climate change are coupled with altered body sizes and growth rates. Glob Chang Biol 22, 3221–3232 (2016).
34. E. Lo Parrino, M. Falaschi, R. Manenti, G. F. Ficetola, All that changes is not shift: methodological choices influence niche shift detection in freshwater invasive species. Ecography 2023, e06432 (2023).
35. L. Gallien, A. H. Thornhill, D. Zurell, J. T. Miller, D. M. Richardson, Global predictors of alien plant establishment success: combining niche and trait proxies. Proc Biol Sci 286, 20182477 (2019).
36. K. Hodgins, D. Bock, L. Rieseberg, Trait evolution in invasive species. Annual Plant Reviews Online 1, 459–496 (2018).
37. P. Lu-Irving, H. E. Marx, K. M. Dlugosch, Leveraging contemporary species introductions to test phylogenetic hypotheses of trait evolution. Current Opinion in Plant Biology 42, 95–102 (2018).
38. L. Wade, Human-Driven Evolution Is a Hallmark of the Anthropocene. Available at: http://www.anthropocenemagazine.org/evolution [Accessed 28 April 2026].
39. K. A. Capps, S. Chapman, K. Clay, J. Fresnedo-Ramírez, D. L. Potts, Reshaping the Tree of Life: ecological implications of evolution in the Anthropocene. Frontiers in Ecology and the Environment 20, 111–116 (2022).
40. C. Lever, Naturalized Fishes of the World (Elsevier Science, 1996).

41. H. Seebens, et al., Global rise in emerging alien species results from increased accessibility of new source pools. Proc Natl Acad Sci U S A 115, E2264–E2273 (2018).
42. J. Gui, L. Zhou, Genetic basis and breeding application of clonal diversity and dual reproduction modes in polyploid Carassius auratus gibelio. Sci China Life Sci 53, 409–415 (2010).
43. G. H. Copp, R. Garthwaite, R. E. Gozlan, Risk identification and assessment of non-native freshwater fishes: a summary of concepts and perspectives on protocols for the UK. J Appl Ichthyol 21, 371–373 (2005).
44. A. Palandačić, L. Kruckenhauser, H. Ahnelt, E. Mikschi, European minnows through time: museum collections aid genetic assessment of species introductions in freshwater fishes (Cyprinidae: Phoxinus species complex). Heredity (Edinb) 124, 410–422 (2020).
45. E. K. Balon, About the oldest domesticates among fishes. Journal of Fish Biology 65, 1–27 (2004).
46. Froese, R.; Pauly, D. (eds.), FishBase. FishBase. Available at: https://www.fishbase.us [Accessed 24 February 2022].
47. M. P. Rincón-Díaz, et al., Traits related to distributional range shifts of marine fishes. J Fish Biol 106, 157–172 (2025).
48. O. J. Luiz, et al., Ecological traits influencing range expansion across large oceanic dispersal barriers: insights from tropical Atlantic reef fishes. Proc Biol Sci 279, 1033–1040 (2011).
49. A. E. Bates, et al., Geographical range, heat tolerance and invasion success in aquatic species. Proc Biol Sci 280, 20131958 (2013).
50. M. A. Kirk, B. R. Hays, C. J. Petranek, The value of the species interaction-abiotic stress hypothesis (SIASH) for invasion biology: using native latitude to explain non-native latitudinal range sizes. Biol Invasions 23, 957–968 (2021).
51. S. Domisch, G. Amatulli, W. Jetz, Near-global freshwater-specific environmental variables for biodiversity analyses in 1 km resolution. Sci Data 2, 150073 (2015).
52. D. M. Richardson, et al., Naturalization and invasion of alien plants: concepts and definitions. Diversity and Distributions 6, 93–107 (2000).
53. R. I. Colautti, H. J. MacIsaac, A neutral terminology to define ‘invasive’ species. Diversity and Distributions 10, 135–141 (2004).
54. T. M. Blackburn, et al., A proposed unified framework for biological invasions. Trends in Ecology & Evolution 26, 333–339 (2011).
55. C. Venditti, A. Meade, M. Pagel, Multiple routes to mammalian diversity. Nature 479, 393–396 (2011).
56. J. Baker, A. Meade, M. Pagel, C. Venditti, Positive phenotypic selection inferred from phylogenies. Biological Journal of the Linnean Society 118, 95–115 (2015).
57. M. Pagel, A. Meade, BayesTraits V5.0.3. (2025). Deposited 2025.
58. A. R. Ives, P. E. Midford, T. Garland Jr., Within-Species Variation and Measurement Error in Phylogenetic Comparative Methods. Syst Biol 56, 252–270 (2007).
59. D. Silvestro, A. Kostikova, G. Litsios, P. B. Pearman, N. Salamin, Measurement errors should always be incorporated in phylogenetic comparative analysis. Methods in Ecology and Evolution 6, 340–346 (2015).
60. M. Sakamoto, C. Venditti, Phylogenetic non-independence in rates of trait evolution. Biol Lett 14, 20180502 (2018).
61. E. Paradis, K. Schliep, ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. Bioinformatics 35, 526–528 (2019).
62. J. Avaria-Llautureo, et al., Historical warming consistently decreased size, dispersal and speciation rate of fish. Nat. Clim. Chang. 11, 787–793 (2021).
63. P.-C. Bürkner, brms: An R Package for Bayesian Multilevel Models Using Stan. Journal of Statistical Software 80, 1–28 (2017).