

Climatic vulnerability of the world's freshwater and marine fishes

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Climate change is a mounting threat to biological diversity¹, compromising ecosystem structure and function, and undermining the delivery of essential services worldwide². As the magnitude and speed of climate change accelerates³, greater understanding of the taxonomy and geography of climatic vulnerability is critical to guide effective conservation action. However, many uncertainties remain regarding the degree and variability of climatic risk within entire clades and across vast ecosystem boundaries⁴. Here we integrate physiological estimates of thermal sensitivity for 2,960 ray-finned fishes with future climatic exposure, and demonstrate that global patterns of vulnerability differ substantially between freshwater and marine realms. Our results suggest that climatic vulnerability for freshwater faunas will be predominantly determined by elevated levels of climatic exposure predicted for the Northern Hemisphere, whereas marine faunas in the tropics will be the most at risk, reflecting their higher intrinsic sensitivity. Spatial overlap between areas of high physiological risk and high human impacts, together with evidence of low past rates of evolution in upper thermal tolerance, highlights the urgency of global conservation actions and policy initiatives if harmful climate effects on the world's fishes are to be mitigated in the future.

Vulnerability of ectothermic organisms to climate change is thought to increase towards the tropics as species living at higher latitudes tend to display broader physiological thermal tolerances^{5,6}. In aquatic environments, the upper thermal limits of ectotherms often closely correspond to their experienced temperatures^{7,8}, suggesting that global warming impacts may be more pervasive in the world's rivers and oceans. Assessing global patterns in climatic vulnerability, however, is currently challenged by limited data availability on physiological thermal traits⁴, and the increasing awareness that thermal tolerances derived from species' realized niches may not adequately reflect fundamental niche limits⁹.

Here, we present a global assessment of climatic vulnerability of ray-finned fishes (Actinopterygii) that integrates physiological-based metrics of sensitivity with future climatic exposure. We compiled upper thermal limits for 485 fish species ($n = 327$ freshwater; $n = 158$ marine) and used a data imputation approach to predict the critical thermal maxima (CT_{max}) for 2,960 species of freshwater ($n = 2,276$) and marine ($n = 684$) fishes based on phylogenetic niche conservatism and accounting for phenotypic variability and local adaptations to experienced temperatures⁸ ($R^2 = 0.89$; see Methods; Supplementary Figs 1–3 and Supplementary Tables 1 and 2). We then tested whether global patterns in the vulnerability of fish faunas to climate change differ between freshwater and marine realms as a result of different biogeography histories and ecological pressures.

We estimated species-specific physiological sensitivity using the warming tolerance⁵, defined as the difference between CT_{max} and the mean temperature of the warmest month experienced by a species across its range ($Thab_{max}$). This was performed for both modern-day (1951–2000) and future climate (2061–2080) scenarios using a multi-model ensemble (Supplementary Table 3). Our results reveal that the distribution of warming tolerance varies considerably both in terms of geography and taxonomy (Fig. 1 and Supplementary Table 4). Upper thermal tolerances increase with decreasing latitude for both freshwater and marine fishes (Supplementary Fig. 4a,b). However, increases in tolerance appear to be outpaced by the latitudinal variations in temperature experienced by species across their ranges ($Thab_{max}$) (Supplementary Fig. 4c,d). As a result, warming tolerances are lowest for marine fishes in the tropics (Fig. 1b). Patterns are more nuanced for freshwater fishes, where the variability in warming tolerance is generally higher compared with marine species, particularly at midlatitudes (30°–50° N) in the Northern Hemisphere (Fig. 1a).

When incorporating future climatic exposure, we find that differences in physiological sensitivities are further exacerbated under both a stabilization scenario of greenhouse gas emissions over time (Representative Concentration Pathway 4.5 (RCP4.5); Supplementary Fig. 5 and Supplementary Table 4b) and an increasing emissions scenario (RCP8.5; Fig. 1c,d and Supplementary Table 4c). Climate change is projected to markedly reduce the warming tolerance for many freshwater fishes across the Northern Hemisphere and be particularly severe for species inhabiting high latitudes. By contrast, the lowest warming tolerances in the oceans are projected for tropical fishes. Despite the inherent uncertainty surrounding the effects of a changing climate on migratory species, our results are not affected by their inclusion (Supplementary Fig. 6 and Supplementary Discussion). There is also little evidence for an association between species' International Union for Conservation of Nature (IUCN) conservation status and either modern-day or future physiological sensitivity (Fig. 1 and Supplementary Table 5), which raises concerns about potential mismatches between current vulnerability assessment systems and emerging climate-related threats¹⁰. The finding that broad-scale patterns of warming tolerance may change as climate warms also emphasizes the importance of considering both intrinsic sensitivity and extrinsic exposure to climate change when evaluating the global conservation status of species.

We further map the physiological sensitivity of fish faunas across the world's river and oceans. This was accomplished by calculating the warming tolerances for each species across its range as the difference between its upper thermal limits (CT_{max}) and the mean temperature of the warmest month within $1^\circ \times 1^\circ$ grid cells under current and future climate. We then averaged the warming tolerances for all species expected to occur in each grid cell to

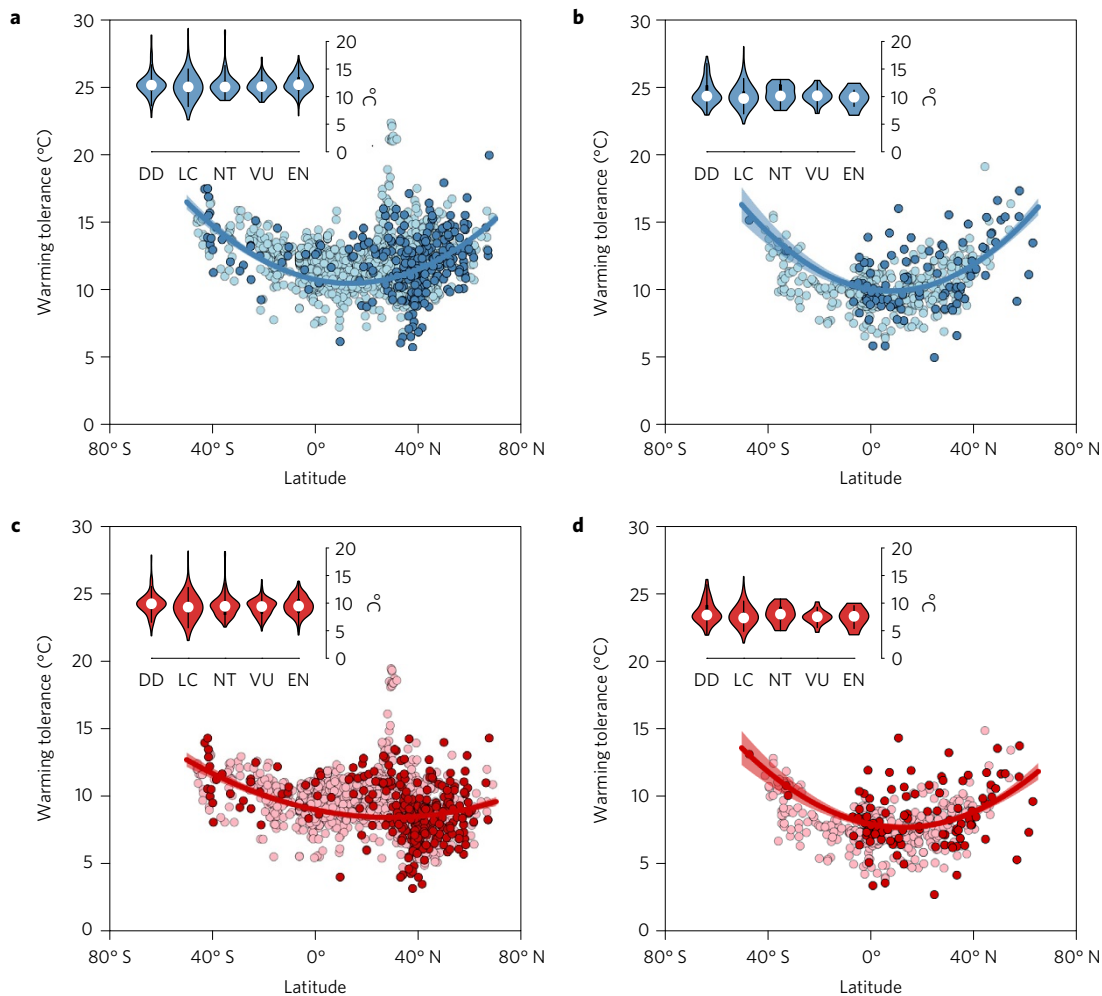


Figure 1 | Species-level patterns in physiological sensitivity for modern-day and projected climate. **a–d**, Warming tolerances according to latitudinal range midpoint for freshwater (**a,c**) and marine (**b,d**) fishes. Blue (**a,b**) represents modern-day (1951–2000) climate and red (**c,d**) represents projected future climate (2061–2080) based on RCP8.5. Lighter colours indicate imputed data. Also shown are the fitted relationships (solid line) and associated confidence intervals (shaded area) using phylogenetic generalized least-squares accounting for uncertainty in CT_{max} from the data imputation procedure (see Methods). The insets display the distribution of the warming tolerances according to the IUCN categories (DD, data deficient; LC, least concern; NT, near threatened; VU, vulnerable; EN, endangered and critically endangered).

produce a faunal-level estimate. We find that current mean warming tolerances in the oceans show a strong and positive association with latitude; a pattern that contrasts with the weak latitudinal trend observed in freshwaters (Fig. 2a,b). These differences in faunal-level warming tolerances can be, in part, explained by distinct distributional patterns observed in the oceans compared with freshwaters (Supplementary Fig. 7). Marine species tend to have broader latitudinal ranges, so that faunas are comprised of more heterogeneous mixes of species-level CT_{max} across latitudes, resulting in relatively invariant patterns of CT_{max} when considered at the faunal level (Supplementary Fig. 7b). As a consequence, lower-latitude faunas in the oceans have lower mean warming tolerance. By contrast, freshwater fishes tend to occupy more limited latitudinal ranges, resulting in faunal-level CT_{max} corresponding more closely to experienced temperatures (Supplementary Fig. 7a). This leads to more similar estimates of mean warming tolerances across latitudes. These differences are likely to reflect the distinct biogeographical histories of freshwater and marine fish faunas. In particular, the presence of spatially uniform warm waters in the oceans favoured the extensive dispersal of tropical species to higher latitudes (that is, ‘out of the tropic’ hypothesis), leading to the decoupling of their thermal and geographic ranges¹¹. In freshwaters, geographic constraints on the distribution of species’ ranges (that is, continental edges and

hydrological barriers) together with the effects of repeated glaciations on high-latitude faunas may have precluded long-distance dispersal in a way similar to marine systems¹².

It follows from the weak trends in modern-day warming tolerances observed in freshwaters that the vulnerability of fish faunas will be more likely to reflect the higher climatic exposure predicted in the Northern Hemisphere (30°–50° N) (Fig. 2c; see Supplementary Fig. 8a for the RCP4.5 scenario). By contrast, the warming tolerances for marine fish faunas in the future are expected to be lower across the tropics (30° S–30° N), mirroring the current patterns in physiological sensitivity (Fig. 2d and Supplementary Fig. 8b). To take into account potential local adaptations to experienced temperature¹³, we also calculated mean warming tolerances using constant species-specific warming tolerances based on the mean temperature experienced by species across their ranges (that is, assuming that CT_{max} varies within species and that warming tolerance is constant across locations, Supplementary Fig. 9 and Supplementary Discussion). Although we find that spatial patterns of warming tolerance are less contrasted between the two realms than in the previous analyses, species in northern high-latitude freshwater basins and tropical oceans remain at greatest risk under projected climate. Our findings are thus consistent with both theoretical¹⁴ and empirical¹⁵ studies suggesting that species loss in

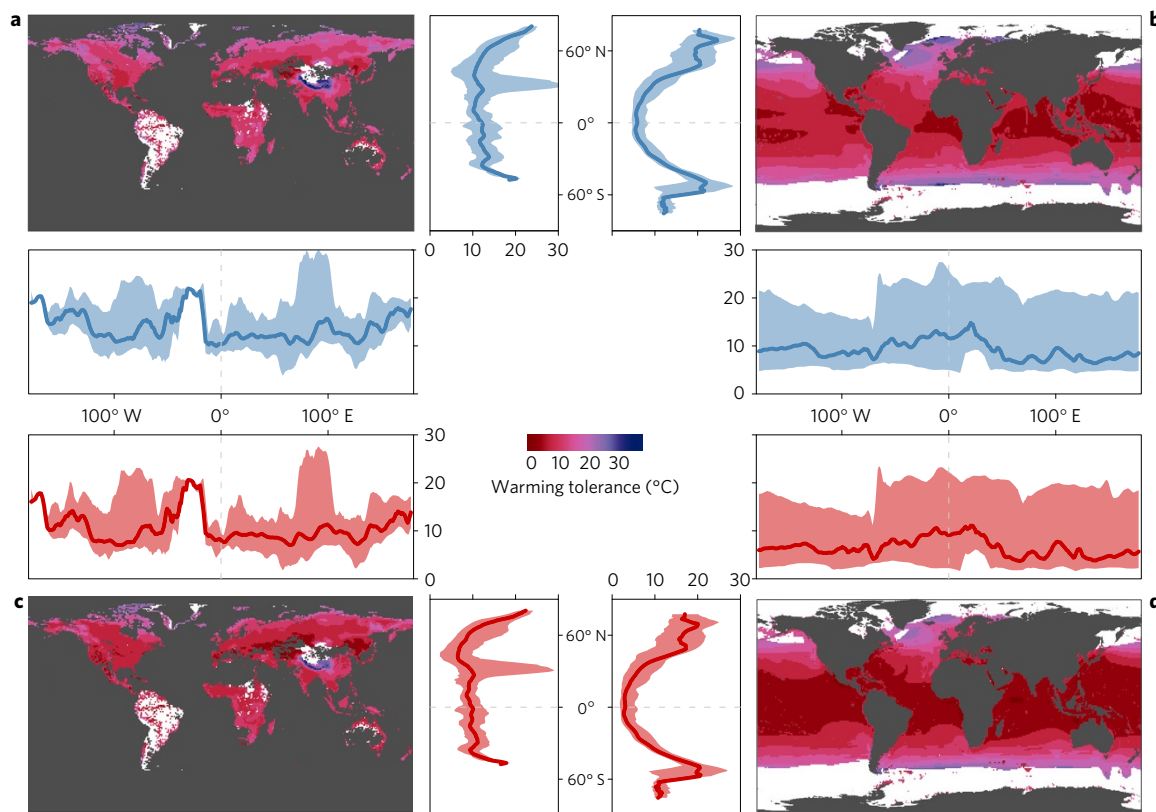


Figure 2 | Faunal-level patterns in physiological sensitivity for modern-day and projected climate. a–d, Mean warming tolerances for freshwater (a,c) and marine (b,d) fish faunas for modern-day (1951–2000) climate (a,b) and projected future climate (2061–2080) (c,d) based on RCP8.5. Mean warming tolerance is calculated for each grid cell on the basis of species' expected occurrences derived from distributional ranges and accounts for uncertainty in CT_{max} from the data imputation procedure (see Methods). Marginal panels are the latitudinal and longitudinal global moving average medians (solid line) and associated 5th–95th percentiles (shaded area) over 5° bands for modern-day (blue) and projected future (red) climate. The grey areas indicate no appreciable flowing freshwaters and white areas indicate missing information.

the marine realm will be prominent in tropical areas. However, the fact that high-latitude freshwater faunas are projected to display the lowest warming tolerances in the future is in contrast to the tropical vulnerability paradigm⁶. Rather, this demonstrates that biogeographical history probably plays an important role¹⁶.

Next, we estimated faunal-level estimates of evolutionary rates based on the differences in CT_{max} across closely related species¹⁷. Although subject to shortcomings, this method offers a tractable estimation of the rates at which climatic niches have evolved in the past that can be applied across many species and compared with projected climatic exposure^{17,18}. We find that the mean rates at which CT_{max} has evolved over the last several million years across fish species (range: 1.9×10^{-5} – $24.9^\circ\text{C Myr}^{-1}$) will be largely outpaced by the projected climatic exposure (RCP8.5; range: 0.01 – $0.06^\circ\text{C yr}^{-1}$) (Fig. 3). Although this result may suggest that marine and freshwater fish faunas are on the brink of experiencing substantial biodiversity losses, we caution that phenotypic traits can respond to environmental changes much more rapidly than what is considered in phylogenetic analyses. Indeed, direct conclusions on adaptability derived from absolute rates of niche evolution overlook temporally fluctuating selection where rapid short-term changes do not accumulate into large long-term phenotypic differences¹⁹. Likewise, the history of Earth's climate has been predominantly warm with shorter intervals of cold climates, and consequently most selective pressures favoured physiological adaptations to lower temperatures⁹. For example, the fact that the faunas displaying the highest mean evolutionary rates are located in the Northern Hemisphere may reflect relaxed selection on CT_{max} for species colonizing from warmer waters, a process that differs

from pushing physiological boundaries. Nonetheless, empirical evidence demonstrates that the degree of macroevolutionary niche conservatism is associated with contemporary species declines²⁰, suggesting that despite these uncertainties, past rates of niche evolution can provide insights into the potential for evolutionary adaptations to enhance species' ability to cope with climate change.

Recognizing that a singular focus on physiological risk is not sufficient to inform robust conservation strategies^{21–23}, we also consider the human context in which climate change is occurring. From a conservation perspective, increasing ecosystem resilience by reducing non-climatic sources of stress (that is, human/societal adaptation strategies) remains a primary objective as mitigating future climate conditions can be best achieved only through international efforts²¹. We therefore quantified the degree of overlap between mean warming tolerances, mean evolutionary rates and human impacts across ecoregions to identify potential priority areas at a scale that can support effective conservation planning efforts while being representative of the biological distinctiveness of the fish faunas (Fig. 4). Our results suggest that many freshwater ecoregions face the double jeopardy of climatic and non-climatic drivers of changes while also comprising faunas with the lowest mean evolutionary rates. Of particular future conservation concern are the freshwater basins located in southern Europe, southeast North America and central Asia. Management interventions should therefore be directed at enhancing habitat quality and connectedness within these areas to maintain evolutionary potential²⁴ and promote niche tracking^{23,25}. Alternatively, where preventing biodiversity losses and improving human livelihoods involves conflicting management decisions, more proactive management strategies such

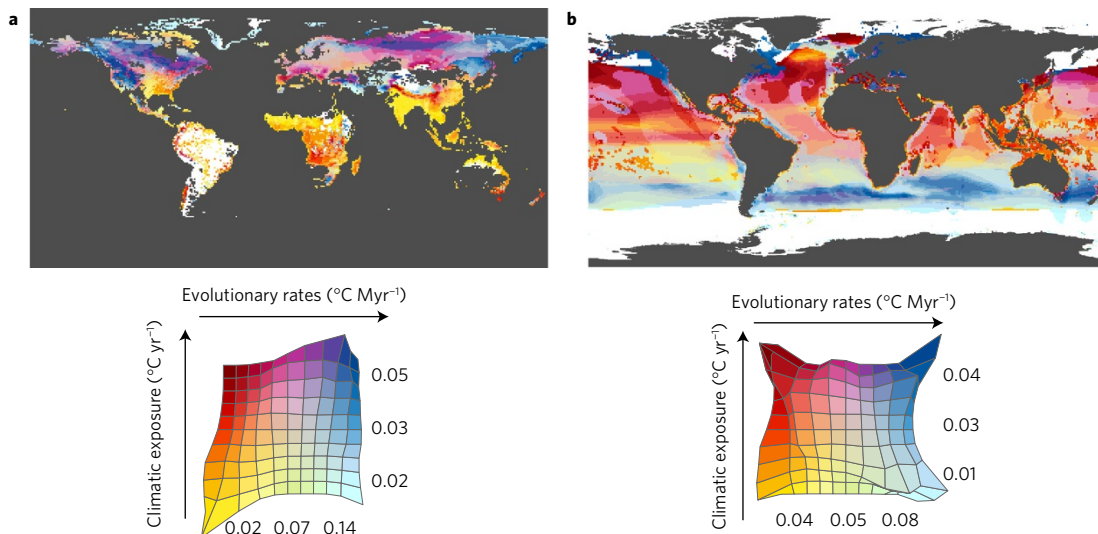


Figure 3 | Comparison between faunal-level evolutionary rates and future climatic exposure. a,b, Mean evolutionary rates versus future climatic exposure for freshwater (a) and marine (b) fish faunas. Mean evolutionary rate is calculated for each grid cell on the basis of species' expected occurrences derived from distributional ranges and accounts for uncertainty in CT_{max} from the data imputation procedure (see Methods). Future climatic exposure is calculated as the difference between projected future climate (2061–2080) based on RCP8.5 and modern-day (1951–2000) climate. The legend indicates the density of grid cells within the 2D colour space defined by the variables broken according to the percentiles of their respective distributions. The grey areas indicate no appreciable flowing freshwaters and white areas indicate missing information.

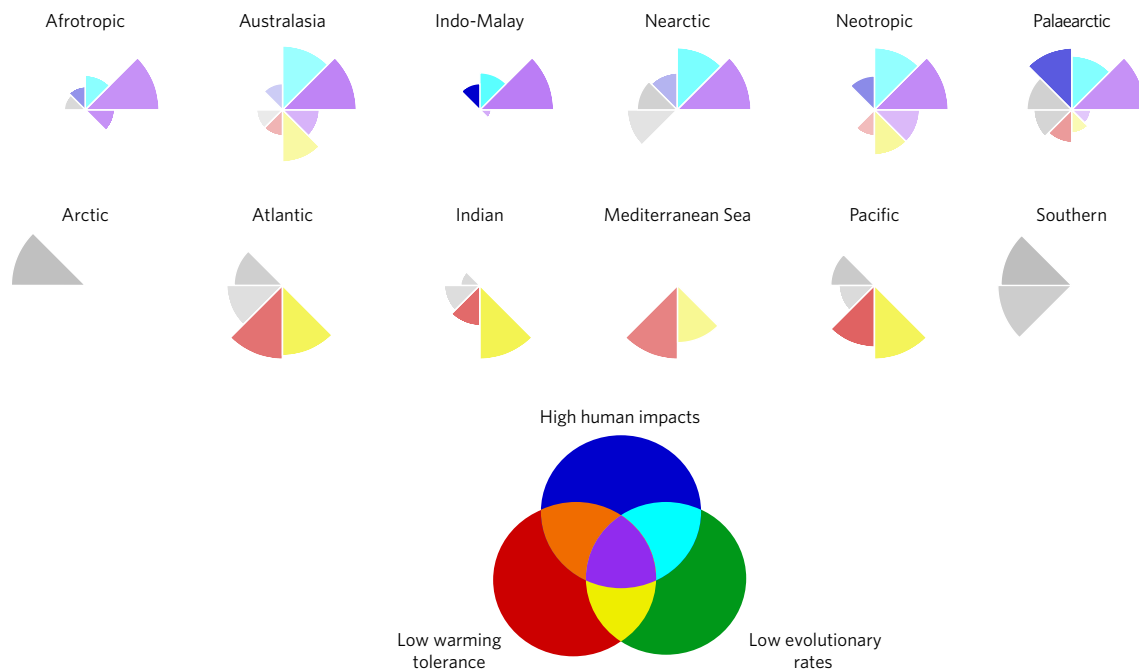


Figure 4 | Spatial overlap between projected physiological sensitivity, evolutionary rates and human impacts. Overlap of mean warming tolerances, mean evolutionary rates and contemporary human impacts within major freshwater (upper panels) and marine (bottom panels) areas. Sectors (that is, wedges) were defined according to the bi-dimensional space formed by the first two axes of a principal component analysis performed on the three variables averaged at the ecoregion scale. The size of the sectors indicates the proportion of ecoregions for each category of overlap and the level of transparency represents the mean magnitude of overlap within this category (see Methods). The grey indicates high mean warming tolerances, high mean evolutionary rates and low contemporary human impacts. Projections of future climate are based on RCP8.5 (2061–2080).

as assisted migration programmes might be envisioned²¹, although the prospect of unintended, unpredictable consequences is still the topic of substantial debate²⁶. We show that climatically vulnerable ecoregions for marine fishes do not necessarily coincide with the areas of highest human impacts. However, the higher projected physiological sensitivity of the marine faunas, especially in the tropical eastern Pacific, central and western Indo-Pacific, together with the fact that their upper thermal limit has been comparatively stable

through evolutionary times, may be indicative of severe impacts in the future. Nonetheless, in the absence of information about genetic variation for the majority of the species included in our analyses and in light of the complex selection pressures likely to be triggered by climate change²⁷, the potential for evolutionary adaptations remains uncertain and represents an important research frontier.

The physiological risks reported in the present study are less dramatic compared with previous estimates derived from realized

niches, where an alarming number of species are predicted to exceed their thermal limits in the future¹⁵. We recognize that in addition to the unavoidable uncertainty coming from the data imputation procedure, our methodology is conservative in the sense that it does not incorporate climatic variability and extreme events, the interacting effects of other climate change components such as flow change²⁸ and deoxygenation²⁹, or the consequences of altered biotic interactions driven by the widespread redistribution of biodiversity^{14,30} (see Supplementary Discussion). Our conclusion concerning the vulnerability of freshwater fish faunas should also be tempered by the relative number of tropical and temperate species included in the analyses (Supplementary Fig. 10 and Supplementary Discussion). Despite these considerations, the present study provides a unique physiological assessment of global patterns in climatic vulnerability for an important group of vertebrates. Future efforts should thus build on the strengths of our approach to fill key gaps in our understanding of climatic risk for additional taxonomic groups and geographical areas.

Methods

Methods, including statements of data availability and any associated accession codes and references, are available in the [online version of this paper](#).

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Author contributions

L.C. and J.D.O. designed the general study, L.C. collected the data and implemented the analyses, and L.C. and J.D.O. wrote the paper.

Additional information

Supplementary information is available in the [online version of the paper](#). Reprints and permissions information is available online at www.nature.com/reprints. Publisher's note: Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations. Correspondence and requests for materials should be addressed to L.C.

Competing financial interests

The authors declare no competing financial interests.

Methods

Climate data. Modern-day (1951–2000) and projected (2061–2080) land and sea surface temperatures were obtained from multi-model ensemble means of five atmosphere and ocean general circulation models that have demonstrated overall good performances at a global scale³¹ (Supplementary Table 3). Future climate scenarios were generated according to the Representative Concentration Pathways RCP4.5 and RCP8.5, available from the World Climate Research Program Coupled Model Intercomparison Project Phase 5 (CMIP5). Monthly climate data over land were converted to stream temperature after removing areas without appreciable flows using previously derived global relationships³². Both annual mean stream and sea surface temperatures of the warmest month were then averaged over the two time periods and adjusted to a $1^\circ \times 1^\circ$ grid resolution (see Supplementary Methods for details).

Upper thermal limits. We compiled upper thermal limits for 485 freshwater ($n = 327$) and marine ($n = 158$) ray-finned fish species from studies that used dynamic (the temperature at which individuals lose critical motor function when exposed to gradual increases: critical thermal maximum CT_{max}) or static (the temperature at which 50% of individuals survive a predetermined duration when exposed to a constant temperature: lethal temperature LT_{50}) methodologies³³. We included only studies reporting acclimation—experimental or collection—temperatures ($n = 2,722$) and adjusted thermal limits with respect to the summer temperatures experienced by species across their range and the differences between metrics (for example, ref. 34), while accounting for species' acclimation ability (Supplementary Figs 1 and 2 and Supplementary Table 1; see Supplementary Methods for details).

Data imputation. We generated an imputed data set of CT_{max} for 2,960 species based on the availability of both phylogenetic³⁵ and distributional³⁶ information for ray-finned fishes. We used a phylogenetic imputation approach³⁷ incorporating phenotypic variation and assuming a phylogenetic correlation between CT_{max} and realized thermal habitat (Supplementary Methods). The best-fitting likelihood model of evolution was selected through a model selection procedure based on the Akaike information criterion. We compared Brownian motion, Pagel's λ and Ornstein–Uhlenbeck (single optimum) models. The lambda model had a better fit, using both the Akaike information criterion and a leave-one-out cross-validation analysis ($R^2 = 0.89$; Supplementary Table 2) and was subsequently used to reconstruct missing values for species across the phylogeny as well as their associated uncertainty arising from phenotypic plasticity and the data imputation procedure (that is, standard deviation; Supplementary Fig. 3).

Patterns in species-level physiological sensitivity. Species' physiological sensitivity to changes in temperature was estimated through the warming tolerance⁵ calculated as the difference between upper thermal limits (CT_{max}) and the mean temperature of the warmest month experienced by species across their ranges ($Thab_{max}$) in modern-day and projected under climate change scenarios ($CT_{max} - Thab_{max}$). Latitudinal patterns in species-specific warming tolerance were then assessed by performing weighted phylogenetic generalized least-squares between the measures of warming tolerance and the latitudinal midpoint of species' distributions, and using the inverse of the variance of the CT_{max} estimates as weights. We included a quadratic term and an interaction with species' realm affinity (freshwater versus marine) to account for nonlinearities and potential differences between rivers and oceans. To ensure a similar distribution across the latitudinal gradient between rivers and oceans, marine species with latitudinal midpoints $> 50^\circ$ S were excluded from the analyses ($n = 11$). We also assessed whether the current conservation status of species corresponds to the threat associated with climate change using inverse-variance weighted phylogenetic generalized least-squares with the IUCN Red List categories³⁶ as an explanatory variable and an interaction with realm affinity. We compared models using likelihood ratio tests using a backward stepwise selection procedure from the full model and reported those after removal of all non-significant effect terms.

Patterns in faunal-level physiological sensitivity. We quantified global-scale patterns in faunal-level physiological sensitivity by calculating the inverse-variance weighted mean in warming tolerances within each grid cell i based on species' occurrences derived from IUCN range maps and the mean temperature of the warmest month in modern-day and projected under climate change scenarios ($CT_{max} - Thab_{max,i}$). We also tested an alternative measure that assumes a constant warming tolerance across species' distribution by calculating for each grid cell the inverse-variance weighted mean of the species-level warming tolerance previously estimated (see Patterns in species-level physiological sensitivity).

Comparison with past evolutionary rates. We compared the rates at which upper thermal tolerances have evolved over evolutionary times across closely related species to future climatic exposure. Past rates of evolution in CT_{max} were estimated as the absolute differences between values of the terminal taxa and the values of their ancestors (time is accounted for by dividing by the age of the ancestors)^{17,18}. To quantify global-scale patterns in faunal-level evolutionary rates, we calculated the inverse-variance weighted mean of evolutionary rates based on species' expected occurrences within each grid cell where the variance of the estimates was calculated as the linear combinations of the uncertainties for terminal and ancestor taxa. Future climatic exposure was calculated for each grid cell as the difference between projected climate and modern-day temperature of the warmest month divided by the number of years using the midpoints of the two time intervals.

Assessing ecoregion vulnerability. We evaluated the spatial overlap between mean warming tolerances, mean evolutionary rates and contemporary human impacts at the ecoregion scale. In the freshwater realm, human impacts were quantified within each $1^\circ \times 1^\circ$ grid cell using an index that quantifies multiple anthropogenic stressors covering catchment disturbance, pollution, water resource development, biotic factors and accounts for downstream impacts³⁸. For the marine realm, we used a similar index resulting from cumulative pressures including fishing, pollution, urban development and aquaculture³⁹. Due to different data sources, we rescaled these variables between 0 and 100. We then performed a principal component analysis (PCA) using the mean values for each ecoregion and classified them according to the degree of overlap between the three variables. This was accomplished by dividing the bi-dimensional space formed by the first two components of the PCA (explaining 78% of the total variability) into eight sectors (that is, wedges) characterized by different categories of overlap defined according to the loading matrix (Supplementary Table 6). We then calculated the proportion of ecoregions per category of overlap within major freshwater and marine areas as well as the mean magnitude of overlap for each category using the mean PCA coordinates of the ecoregions within this sector. We used the marine ecoregions of the world⁴⁰ for the coasts and shelves coupled with the pelagic provinces of the world⁴¹ for the surface pelagic waters and the freshwater ecoregions of the world⁴².

Data availability. Collected and imputed data sets can be found at <https://figshare.com/s/eca5d4c047e8c87172db>.

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