



Universiteit
Leiden
The Netherlands

Climate warming drives thermal shocks and accelerated freshwater habitat fragmentation

Wang, H.; Liu, J.; Holden, J.; Chen, P.; Barbarossa, V.; Klaar, M.

Citation

Wang, H., Liu, J., Holden, J., Chen, P., Barbarossa, V., & Klaar, M. (2026). Climate warming drives thermal shocks and accelerated freshwater habitat fragmentation. *Nature Climate Change*, 16(9), 1061-1067. doi:10.1038/s41558-026-02731-9

Version: Publisher's Version

License: [Creative Commons CC BY 4.0 license](https://creativecommons.org/licenses/by/4.0/)

Downloaded from: <https://hdl.handle.net/1887/4310360>

Note: To cite this publication please use the final published version (if applicable).

Climate warming drives thermal shocks and accelerated freshwater habitat fragmentation

Received: 4 July 2025

Accepted: 21 July 2026

Published online: 24 August 2026

**Hong Wang (王泓)**^{1,2}, **Junguo Liu (刘俊国)**^{1,3,4}✉, **Joseph Holden**^{1,2}, **Penghan Chen (陈鹏翰)**¹, **Valerio Barbarossa**^{5,6} & **Megan Klaar**²

Climate change is exposing freshwater fish to warmer temperatures, causing widespread range contraction and population declines. However, how climate-driven disruptions will affect freshwater fish persistence under future thermal extremes remains poorly understood. Here, using weekly water temperature data (1976–2099), we assess the vulnerability of 9,809 freshwater species to short- and long-term thermal extremes and show that gradual warming can trigger abrupt thermal exposure. Tropical regions experience a high proportion of species at risk, whereas non-tropical regions face severe thermal extremes. We introduce the concept of thermal fragmentation exposure to understand how heterogeneous warming fragments freshwater habitat, thereby amplifying local extinction risks. Around 63% of riverine fish will experience more persistent thermal barriers under a high-emissions scenario, with thermal fragmentation accelerating over time. These findings underscore the urgent need for targeted conservation strategies to safeguard freshwater fish biodiversity.

Anthropogenic climate change is exacerbating extreme thermal events, exposing freshwater fish to dangerous temperatures^{1–3}. These extreme events can be both short-term, with high exposure intensity within a single year, and long-term, through prolonged exposure over multiple years^{1,3,4}. While fish may buffer some threats, the accumulation of ‘ecological debt’⁵—especially from consecutive, high-intensity thermal events—remains a major concern⁶. Episodes of extremely hot temperatures have already increased, resulting in widespread mortalities in many fish species^{7–9}. Such events are likely to pose a considerable threat to biodiversity in the coming decades¹⁰. Evaluating the impacts of both short-term and long-term extreme thermal events on biodiversity is, therefore, an urgent conservation priority in the face of rapid anthropogenic climate change^{9,10}.

As temperatures gradually rise, the proportion of species exposed to extreme thermal events will increase^{1,10}. A gradual increase in thermal

exposure allows more time for species to adapt through dispersal or evolutionary processes, and provides greater opportunities to implement conservation interventions and adaptation strategies before the adverse effects of thermal exposure become severe^{11,12}. In contrast, a rapid increase in exposure risk could overwhelm ecological and evolutionary buffering mechanisms, reducing species’ ability to cope with changing conditions^{11,12}. Therefore, understanding the temporal dynamics of exposure is crucial^{11–13}. Recent continental and global studies have provided assessments of climate change impacts on freshwater fish^{1,2}. However, they often lack a temporal perspective, typically presenting the number and locations of species at risk based on static snapshots under different warming scenarios. By analysing the temporal profile of accumulative exposure, we can determine whether the impacts of long-term extreme events propagate gradually or abruptly, and identify the critical time points for intervention^{12,13}.

¹School of Environmental Science and Engineering, Southern University of Science and Technology, Shenzhen, China. ²water@leeds, School of Geography, University of Leeds, Leeds, UK. ³Yellow River Research Institute, North China University of Water Resources and Electric Power, Zhengzhou, China. ⁴Henan Provincial Key Laboratory of Hydrosphere and Watershed Water Security, Zhengzhou, China. ⁵Institute of Environmental Sciences, Leiden University, Leiden, the Netherlands. ⁶PBL Netherlands Environmental Assessment Agency, the Hague, the Netherlands. ✉e-mail: liujunguo@ncwu.edu.cn

Freshwater ecosystems are particularly vulnerable to climate warming as most aquatic organisms are ectothermic and confined to dendritic networks, where dispersal is limited to rivers^{1,4}. As water temperature increases unevenly across different river reaches under climate change, freshwater fish with specific physiological thermal tolerances may find their once-continuous thermal habitats fragmented into isolated patches. Such thermal barriers restrict species dispersal^{15,16}, feeding^{17,18}, reproduction^{15,19} and the ability to escape thermal stress²⁰. Despite its importance, methods for quantifying fragmentation caused by thermal barriers within hydrological networks remain underdeveloped.

Here we distinguish between two types of extreme thermal events. Short-term extreme thermal events are defined as any period during which average weekly water temperatures exceed a species-specific threshold for at least three consecutive weeks (Methods). This threshold represents the mean of the highest weekly temperatures experienced by the species across its geographical range during a historical baseline period (1976–2005) (Extended Data Fig. 1). Long-term extreme thermal events refer to the consecutive occurrence of short-term extreme events for 5 or more years (Methods). To evaluate the impacts of short-term extreme thermal events, we assess their intensity (Extended Data Fig. 1), while for long-term extreme thermal events, we use magnitude, abruptness and timing, providing a cumulative view of thermal stress for species over time (Extended Data Fig. 2). Here magnitude refers to the maximum cumulative percentage of species in an assemblage (that is, species in ~ 100 km² grid cells) under long-term thermal exposure. Abruptness measures how concentrated this exposure is in time, calculated as the percentage of newly exposed species occurring in the decade of maximum exposure, scaled by magnitude. Timing is defined as the midpoint of that decade.

We introduce the concept of thermal fragmentation exposure (TFE), the climate-driven disruption of thermal habitat continuity across river networks, to represent a substantial yet underappreciated risk caused by thermal barriers through heterogeneous warming at the species level for freshwater fish biodiversity. TFE is defined using the intensity of short-term extreme thermal events in river reaches, with more intense exposure indicating more severe thermal barriers. High-intensity events may function as thermal blocks, directly hindering population dispersal or migration in search of suitable thermal conditions (Methods). Collectively, our framework reveals global patterns of assemblage- and species-level exposure to future thermal extremes in freshwater ecosystems.

Assemblage-level spatiotemporal dynamics of thermal exposure

Under a high-emissions scenario (Representative Concentration Pathway (RCP) 8.5), 63% of global fish assemblages are projected to have at least one species exposed to prolonged unprecedented extreme temperatures (beyond a species-specific threshold for 5 consecutive years) before 2100, compared with 38% under a median emission scenario (RCP4.5) and 25% under a low-emissions scenario (RCP2.6) (Fig. 1). Thermal exposure magnitude and intensity exhibit distinct spatial patterns (Fig. 1). High exposure magnitude (>50%) with low thermal intensity (<50%) is concentrated in the tropics, while high thermal intensity with low exposure magnitude is mostly observed at higher latitudes. Specifically, under RCP8.5, 46% of fish assemblages in tropical areas will have over half of their species exposed to prolonged unprecedented temperatures by 2100, compared to 16% in non-tropical areas (Fig. 1a,b). In contrast, high exposure intensity is more of a threat to non-tropical areas, with 54% of fish assemblages affected, compared to 30% in the tropics in the 2090s (Fig. 1a,b). This pattern of higher exposure magnitude in tropical regions and higher exposure intensity in non-tropical regions holds under RCP4.5 (and RCP2.6) (Fig. 1c–f). In tropical regions, 17% (9%) of areas experience high exposure magnitude, compared to 5% (2%) in non-tropical regions. In contrast, high

thermal intensity affects 6% (3%) of tropical regions, while 27% (17%) of non-tropical regions are impacted (Fig. 1c–f).

Regions with high species richness face distinct threats. Southern Europe and eastern North America will experience high thermal intensity under both RCP2.6 and RCP4.5 (Fig. 1c,e). Under RCP8.5, rising emissions substantially increase thermal exposure magnitude in their southern regions, leading to both high exposure magnitude and intensity (Fig. 1a). In contrast, tropical regions with high species richness, such as the Amazon, Congo and Southeast Asia, are primarily threatened by high thermal exposure magnitude, except for downstream areas of the Amazon, Mekong and Chao Phraya rivers (Fig. 1a).

The magnitude of thermal exposure is greatest in the tropics (Fig. 1), where narrow historical climate variability and thermal gradients suggest that many species are already close to their upper thermal limits across much of their geographic range¹². In contrast, lower exposure magnitudes in higher latitudes reflect greater warming tolerance (Fig. 1), indicating a greater thermal safety margin to adapt to rising water temperatures^{21,22}. Thermal exposure intensity poses a more notable threat to species at higher latitudes. While only a small proportion of species in these regions exceed their species-specific thresholds, this can lead to devastating consequences when an extreme thermal event occurs. Previous research has shown that one extreme thermal event can have catastrophic impacts on Pacific salmon and white sturgeon in Alaska⁷ and British Columbia^{3,23}.

The most striking feature of exposure for local assemblages is its abruptness (Fig. 2). Projected thermal exposure will not occur gradually. Instead, increasing thermal exposure magnitudes are characterized by periods of relative stability punctuated by sudden increase, where large numbers of species in assemblages are exposed in a narrow time window. Under RCP8.5, mean abruptness is 64%, meaning that nearly two-thirds of ultimately exposed species become newly exposed within the decade of maximum exposure, with high values concentrated in the Amazon, southeastern North America and the Indian subcontinent (Fig. 2a). The proportion of fish assemblages experiencing abrupt thermal exposure was reduced by half with each step down in emission scenario, while mean abruptness slightly increased (70% under RCP4.5 and 75% under RCP2.6; Fig. 2b,c). These patterns of abruptness suggest that even gradual climate warming results in near synchronous thermal exposure in an assemblage, regardless of scenarios.

Under higher-emission scenarios, the decade of maximum exposure occurs later in the century but involves a sharper increase in the number of exposed species (Fig. 2). Under RCP8.5, threatened assemblages emerge widely after 2060, when new exposure increases rapidly across many regions (Fig. 2a,d). Although the timing of abruptness occurs later under a higher-emission scenario (Fig. 2d,f), this does not imply that high emissions delay the onset of abruptness. Instead, the lag between peak emissions and the emergence of abrupt thermal exposure underscores the urgent need for early and effective mitigation measures to prevent high-magnitude abruptness. Together, the magnitude, abruptness and timing of exposure describe the temporal evolution of the accumulating number of co-occurring species exposed to thermal conditions exceeding their species-specific thresholds. This does not necessarily mean direct local extinction, as species' fundamental niche limits are often broader than their realized niche limits, providing buffering against immediate local extinction¹². Nevertheless, these dynamics reveal distinct spatial patterns and critical timings when the risk of local extinction, while not inevitable, could abruptly escalate, indicating that species persistence in the wild is severely compromised¹².

TFE at the species level

To capture climate-induced risks arising from spatially heterogeneous thermal regimes and warming across river networks, we propose the TFE concept at the species level. We extracted the river network

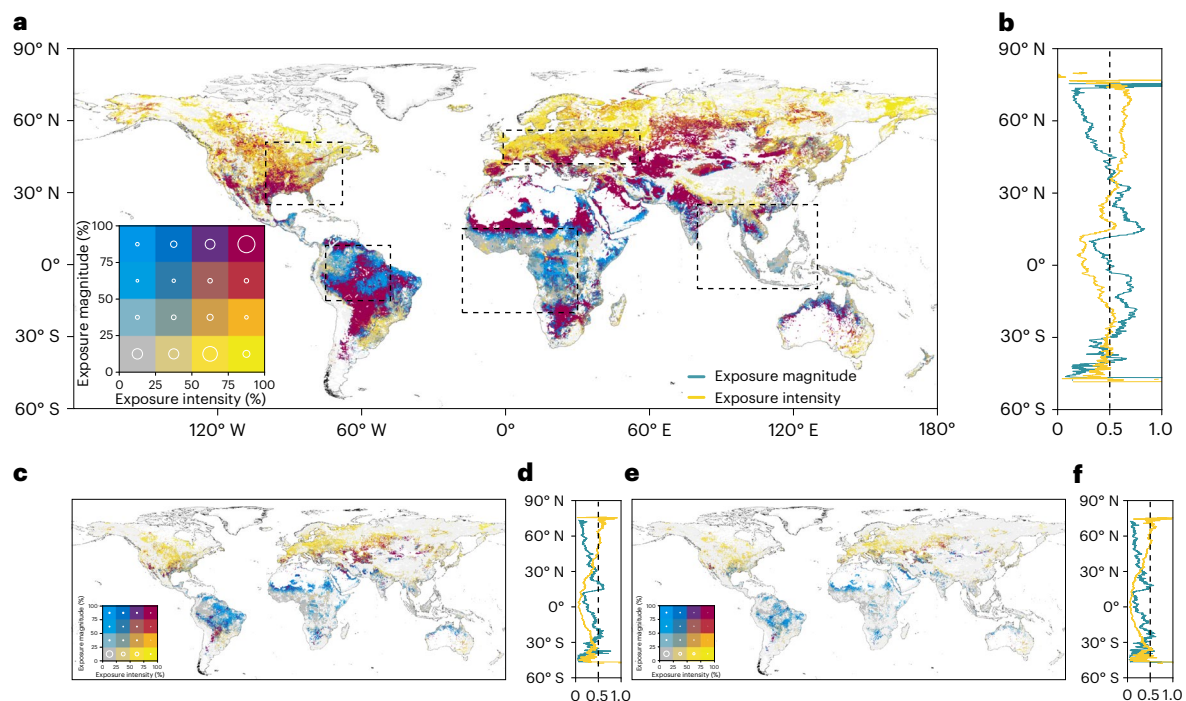


Fig. 1 | Spatial patterns of freshwater fish assemblages' thermal exposure magnitude and intensity due to extreme thermal events by 2099. a–f, Bivariate maps (a,c,e) and latitudinal distributions (b,d,f) showing the exposure intensity scaled to blocking probability (x axes of insets, %), indicating the severity of short-term thermal extremes, and exposure magnitude as the proportion of species exposed as a percentage of local species richness (y axes of insets, %) across high- (a,b, RCP8.5), intermediate- (c,d, RCP4.5) and low-emissions (e,f, RCP2.6) scenarios. The circles in each inset indicate the proportion of

assemblages (species in $\sim 100 \text{ km}^2$ grid cells) within each bivariate bin. The boxed regions in a are those where there is a concentration of high species richness per grid cell. Latitudinal curves were generated by quantifying the mean of grid cells for exposure magnitude and exposure intensity in each 5-arcminute latitudinal band with valid values (in b, d and f). The maps show median estimates from five climate models. White areas denote no data areas (no species occurring or no data available), and light grey regions indicate thermal refugia, where no species experience thermal exposure by 2099.

and flow direction for 9,809 species, extending beyond their current geographic ranges to include all hydrologically connected grid cells. Our results show that climate-driven changes in TFE (ΔTFE) vary among species and across emission scenarios, time periods and climate zones (Fig. 3 and Extended Data Fig. 3). While the threshold of habitat fragmentation above which imperiled species' survival remains uncertain, 20% is considered to indicate a high risk (Methods). Under RCP2.6, the proportion of species with high ΔTFE ($>20\%$) increases from 5% in the 2020s to 13% in the 2050s, followed by a slight decrease to 12% by the 2080s (Fig. 3d). In contrast, under RCP8.5, the proportion of species with high ΔTFE rises from 7% in the 2020s to 40% in the 2050s, then drastically increases to 81% by the 2080s (Fig. 3d). Notably, without constrained emissions, the proportion of species at high risk of ΔTFE in the mid-century (2050s) under RCP8.5 would already exceed the proportion of species at risk (36%) projected for the 2080s under RCP4.5. The global summaries of ΔTFE highlight that RCP2.6 will delay the most-at-risk species ($\Delta\text{TFE} > 20\%$) under TFE by 68 years compared to RCP8.5, providing an adaptation window for 72% of species (Fig. 3e). ΔTFE patterns also differ among climate zones (Extended Data Fig. 3). Tropical species show consistently lower proportions of high ΔTFE , likely because their generally higher species-specific thresholds reduce the intensity of short-term thermal extremes and occurrence of thermal blocks; by contrast, temperate- and cold-region species show higher ΔTFE , reflecting their greater sensitivity to high-intensity short-term extremes. Species in arid regions also face substantial risk from high-intensity short-term thermal extremes, despite their relatively high species-specific thresholds.

Across all emission scenarios we found that $>20\%$ of species will experience over half of their TFE increase outside their current geographic ranges between 2005 and 2040 (Fig. 3f and

Extended Data Fig. 4). This highlights the critical role of rivers beyond present ranges in maintaining thermal connectivity during the early stages of climate change. During this period, most within-habitat river segments have suitable thermal conditions, continuing to provide a thermal connectivity function for species and contributing less to the initial TFE increase. However, in later decades, as temperatures exceed species-specific thresholds, direct habitat loss within species' geographic ranges will become the dominant driver of TFE increase.

Previous analyses of the biodiversity crisis under climate change focused on the total geographic range of species exposed to temperatures above species-specific thresholds, emphasizing the risks of global extinction¹¹. However, local extinctions often provide an early warning, offering an opportunity for preventative conservation. While some studies have quantified species loss at the assemblage level to assess local extinction risk^{1,12}, TFE provides a complementary perspective designed for freshwater fish at a species level by explicitly incorporating the climate risk caused by heterogeneous thermal regimes and warming in dendritic river networks. This metric reflects the limited ability of populations to access suitable thermal refugia and indicates reduced species persistence due to limited dispersal and disrupted genetic connectivity (Fig. 3).

We classified TFE trends under RCP2.6, RCP4.5 and RCP8.5 into no-trend and trend-based types according to their temporal shapes (Fig. 4). These classes were then used to summarize dominant TFE responses across species and scenarios (Fig. 5). TFE change patterns differ considerably among species under RCP2.6—40% of species experience stable TFE patterns (23% stable constant, 17% stable concave), whereas 34% exhibit a linear increase, 14% an abrupt increase and 12% a decelerating increase trajectory. Under RCP4.5, the proportion of

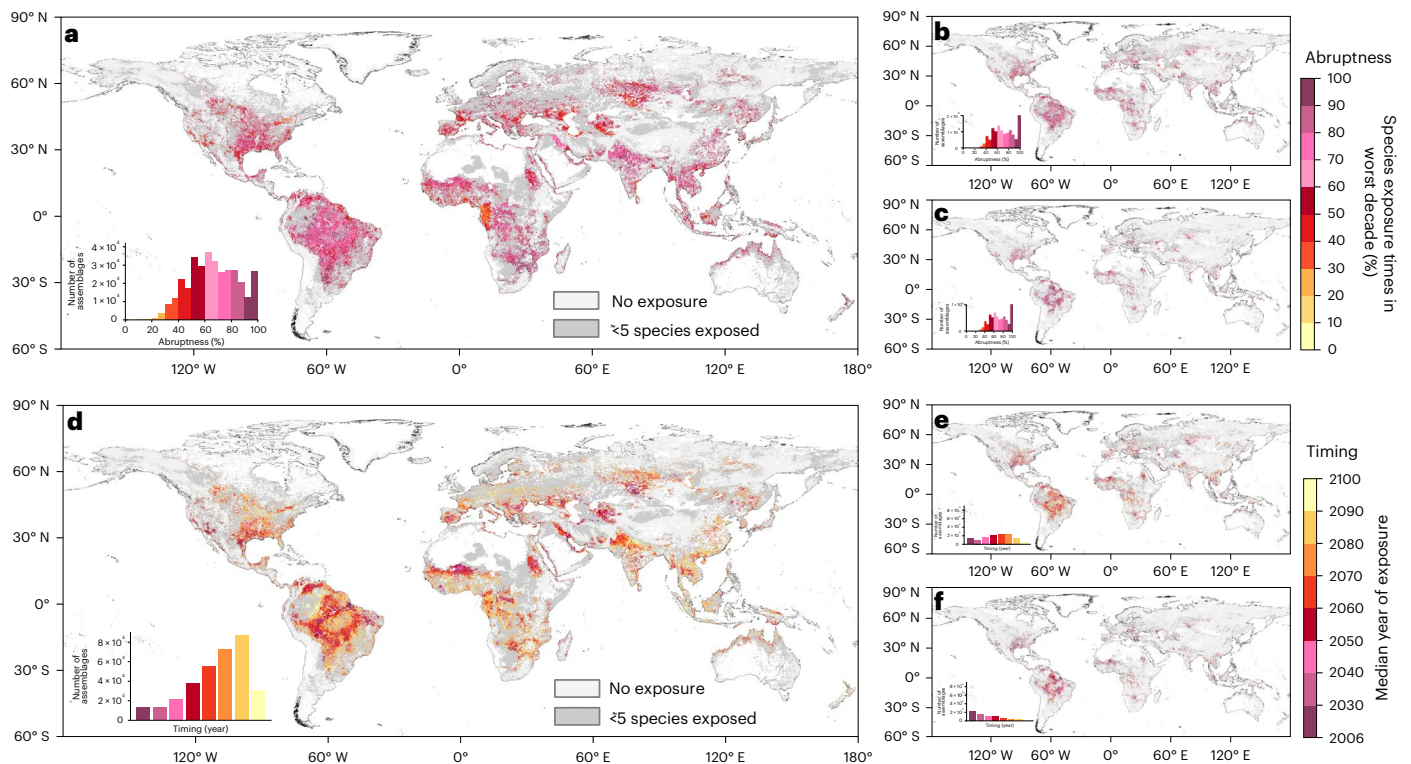


Fig. 2 | Spatial distribution of abruptness and timing of exposure for local assemblage. **a–c**, Abruptness of exposure. **d–f**, Timing of exposure. Maps show the median values across five climate models under high- (**a,d**, RCP8.5), intermediate- (**b,e**, RCP4.5) and low-emissions (**c,f**, RCP2.6) scenarios. Grey

regions represent assemblages with less than five species exposed. Insets: the distribution of abruptness and timing across all assemblages, with colours corresponding to the scale bars. Light grey regions indicate thermal refugia, where no species experience thermal exposure by 2099.

species experiencing increasing trends rises sharply. Notably, 67% of species are projected to follow a linear-increase trajectory, and 18% experience an abrupt increase. Only 1% of species remain in a stable constant trajectory under RCP4.5. Under RCP8.5, 63% of species shift to an accelerating-increase trajectory, and 65% of species experiencing a linear increase under RCP4.5 transition to an accelerating-increase trajectory under RCP8.5, highlighting the non-linear effect of warming on thermal fragmentation. Additionally, 12% of species retain a decelerating-increase trajectory, while abrupt-increase patterns persist in 6% of species under RCP8.5, with 56% of these transitioning from a linear-increase trajectory under RCP4.5.

Under RCP2.6, warming plateaus by the middle of the century, resulting in a shorter duration of temperature increases compared to higher-emission scenarios. Consequently, thermal exposure remains relatively stable, with no significant trends, as only grid cells near species-specific thresholds will experience exposure. The intensity remains insufficient to create thermal blocks but gradually increases the thermal cost of movement through river reaches. Under RCP4.5 and RCP8.5, global temperatures increase throughout the century, driving high-magnitude TFE that continues to accumulate for many decades.

Although trajectory classification revealed broad trend transitions, we emphasize the importance of TFE fluctuations, since optimal temperatures between short-term extreme thermal events create ‘windows of opportunity’ for species to recover. We observed that the temporal autocorrelation of TFE increased with emissions (Extended Data Fig. 5). The skewness of temporal autocorrelation distribution shifted from 0.03 to -0.61 , transitioning to left-skewed as emission increases. This shift indicates more species will experience persistently increasing TFE with less temporal variability, suggesting the erosion of temporal refugia and the prevention of temporal rescue effects for species, ultimately increasing extinction risk^{24,25}.

Vulnerability assessment

Here we assess, at the global scale, the threat of future short-term and long-term extreme thermal events for 9,809 freshwater lotic fish species. We find that tropical species face greater thermal exposure risks from long-term thermal stress, while non-tropical species are more vulnerable to short-term thermal exposure with high intensity. Tropical freshwater species often have narrow thermal safety margins, such that even modest warming can cause mortality^{21,22}. For instance, widespread fish mortality was recorded during the 2023 Amazon Basin heatwave–drought event, where elevated temperatures and associated hypoxia led to tens of thousands of fish fatalities, including *Hypophthalmus edentatus*^{26–28}. The projected long duration and high frequency of short-term extreme events (Supplementary Figs. 1 and 2 and Supplementary Text 1), along with the high magnitude and abruptness of long-term thermal exposure (Figs. 1 and 2a–c), pose a major threat to tropical fish assemblages. In contrast, climatic vulnerability in non-tropical regions is primarily driven by the intensity of short-term extreme thermal events (Fig. 1 and Supplementary Fig. 3). These findings highlight the importance of considering climatic variability and temporally dynamic perspectives in conservation-relevant assessments.

Consistent with findings from terrestrial and marine ecosystems, a linear rate of warming does not result in a gradual increase in cumulative species exposure at the assemblage level^{11–13}. Instead, we observe a pervasive pattern of abruptness, suggesting ecological disruptions driven by long-term extreme events are more likely to occur suddenly with future warming, particularly under RCP8.5. While the magnitude of exposure is lower in RCP4.5 and RCP2.6, abruptness still occurs in certain regions such as the Amazon and southeastern North America. This pattern arises because species with overlapping geographic range often share similar realized thermal limits, regardless of warming rate¹².

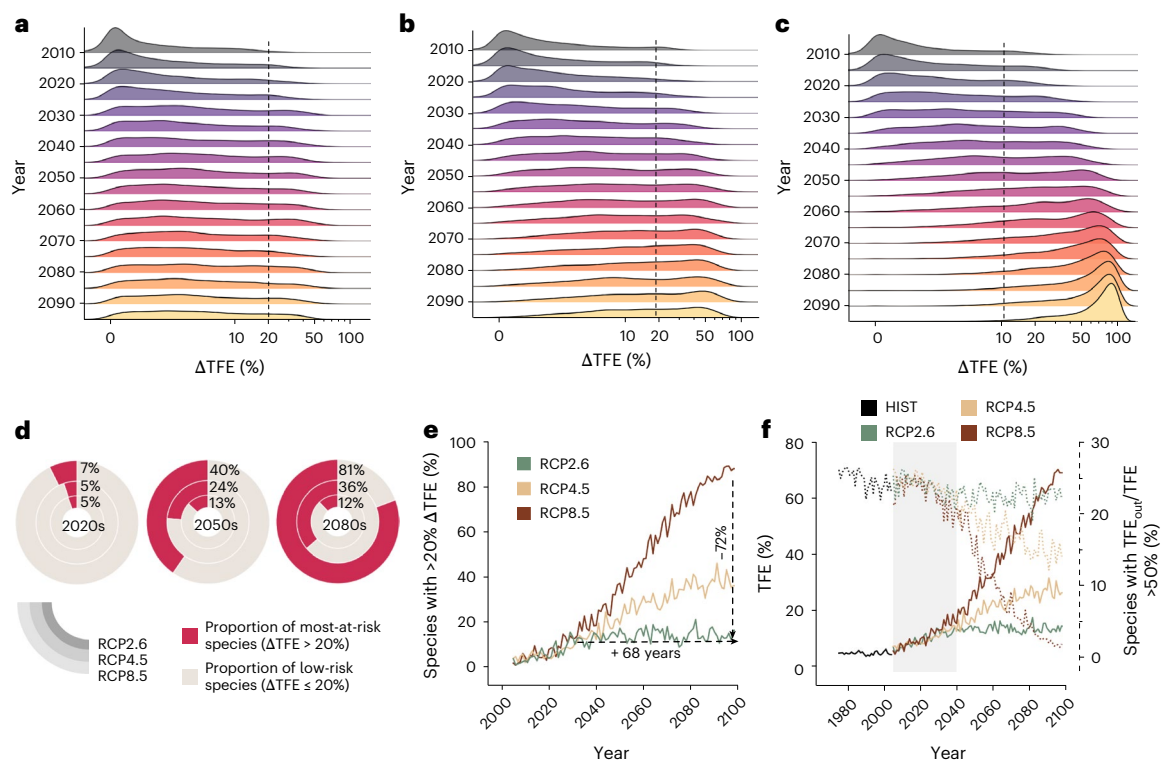


Fig. 3 | Comparison of TFE among species across different periods and scenarios. **a–c**, Distribution of the change in mean TFE (Δ TFE) for fish species every 5 years from 2010 to 2099, with colours transitioning from grey to yellow, under low- (**a**, RCP2.6), intermediate- (**b**, RCP4.5) and high-emissions (**c**, RCP8.5) scenarios compared with the historical period (1976–2005). The probability density of Δ TFE distribution is log transformed. **d**, Pie charts illustrating the proportion of most-at-risk species (Δ TFE > 20%, red) during the 2020s

(2010–2039), 2050s (2040–2069) and 2080s (2070–2099) under RCP2.6, RCP4.5 and RCP8.5 (from inner to outer circle). **e**, Time evolution of the proportion of species at high risk (Δ TFE > 20%) due to TFE. **f**, Time series showing TFE (left y-axis, solid lines) and the proportion of species with >50% of their TFE occurring outside their habitats (right y-axis, dashed lines) for the historical period (HIST) and future emission scenarios. Grey shading indicates the early scenario period (2005–2040).

Trajectory classification	No trend (stable)	Trend (decrease or increase)
Smooth	Constant Convex Concave	Linear Accelerate Decelerate
Abrupt		

Fig. 4 | Trajectory shapes with associated properties. TFE trajectories were classified into three no-trend types—stable constant, stable convex and stable concave—and eight trend-based types. The trend-based types include two linear changes (linear increase, linear decrease), four non-linear patterns (increase or decrease decelerate, increase or decrease accelerate) and two abrupt changes (abrupt increase, abrupt decrease).

Early warning management system

Previous studies have largely emphasized physical barriers, such as dams, that fragment fish habitats^{29,30}. Here we introduce a new perspective by quantifying climate-driven fragmentation for freshwater fish in dendritic river networks. Our findings of species-level TFE reveals a dominant trend shift from no change to a linear increase, ultimately accelerating as emissions rise. Fewer species are projected to experience TFE fluctuations under higher emission rates. The reduction in fluctuations suggests a decline in protective temporal refugia, limiting species' ability to recover from thermal stress^{24,25}. Consequently, populations may face heightened extinction risks due to prolonged and high TFE driven by climate change. Nonetheless, physical barriers such as dams and reservoirs can also influence thermal connectivity by altering flow regimes and water temperatures^{31–33}. These effects

could either amplify or dampen TFE, depending on flow regulation. The FutureStreams dataset used here incorporates reservoir effects, partly accounting for temperature modifications caused by flow regulation³⁴. Improved reservoir management could be a future tool for managing risks from abrupt changes in TFE in some locations³³.

To enhance understanding of the climate risks to species and inform conservation strategies, concepts such as climate connectivity and climate velocity were previously developed^{35–40}. Climate connectivity, which incorporates landscape structure and climate conditions to identify pathways to facilitate species movement in response to shifting climate, has been extensively studied in terrestrial and marine ecosystems^{35–37}. Similarly, climate velocity relies solely on environmental and climate data to indicate the direction and speed that species need to move to track their current climate niche^{38–40}. However, warming can create thermal barriers that disrupt species' dispersal by increasing metabolic costs or altering their orientation⁵ (Supplementary Table 2). These thermal barriers may slow or even prevent species from tracking shifting isotherms⁵. Species-level TFE fills this gap by integrating climate data, river network structure and species-specific physiological tolerance to assess climate vulnerability for freshwater fish.

We do not account for acclimation capacity within or across generations, evolutionary adaptation or species-specific dispersal ability, though these processes play a crucial role in determining species' resilience to climate change^{41–43}. Instead, we focus on the spatial and temporal dynamics of thermal exposure risk, which ultimately shape species' acclimatization, adaptations and dispersals processes. We acknowledge that species-specific thresholds derived from long-term average maximum weekly water temperatures within species' realized

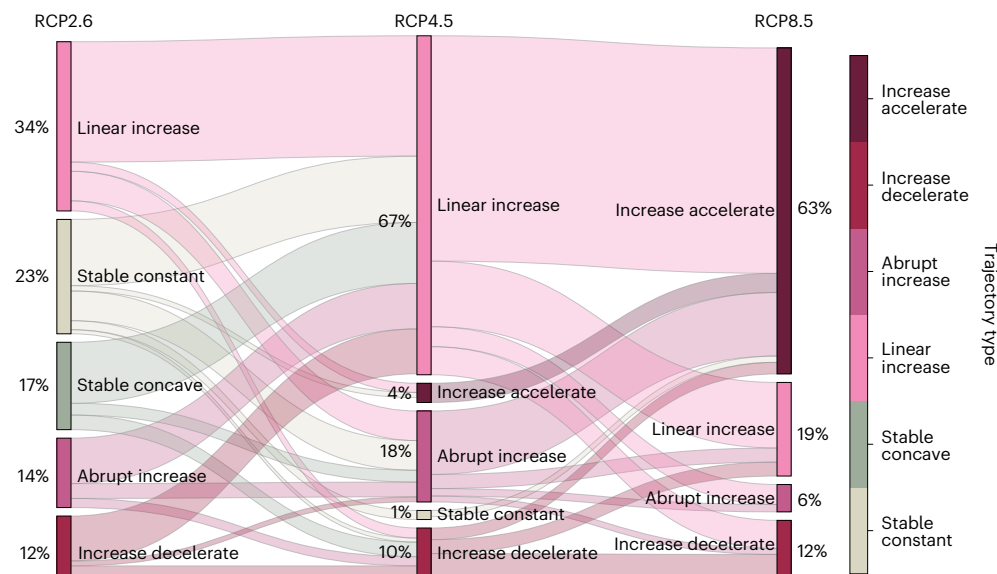


Fig. 5 | TFE trajectory transitions for species under low- (RCP2.6), intermediate- (RCP4.5) and high-emissions (RCP8.5) scenarios. TFE trajectory is the median TFE from five climate models during 2005–2099. For clarity, only species trajectories with a flow size greater than 50 species are shown, excluding 254 species from this diagram.

thermal niches may underestimate their actual critical thermal limits, especially for small-ranged species (Extended Data Fig. 6). However, using realized niche limits provides a precautionary approach that is widely applied for estimating species exposure to climate change^{1,11–13}. Likewise, applying a single dispersal kernel globally introduces species-level and basin-specific uncertainties, representing a neutral approximation rather than a mechanistic movement model. Because dispersal abilities vary widely among species, this approach may overestimate TFE for diadromous or highly migratory taxa, and underestimate TFE for extremely sedentary, headwater-restricted species. The global TFE framework should, therefore, be regarded as a first-step screening and prioritization tool, rather than as a definitive risk assessment, until validated with additional regional and species-specific data (Supplementary Text 2 and 3). Nevertheless, species-level TFE trajectories reveal a previously unexamined dimension of vulnerability—that is, whether a species can withstand the increasing thermal exposure arising from heterogeneous thermal regimes and warming due to more frequent thermal extremes across the river network. In addition, our analyses focus on how warming shifts thermal barriers that affect the thermal connectivity of the extent of occurrence (EOO) where species are currently known to occur (Supplementary Text 2 and Extended Data Figs. 7 and 8). Although some species may experience reduced TFE under future warming by shifting their ranges to track suitable climates, such range shifts are not modelled here. Nevertheless, mapping thermal barriers with TFE values provides additional spatial context to inform future assessments of potential range expansion and recolonization under climate change.

Our analysis serves as an early warning system, identifying the magnitude, patterns and timing of suitable habitat loss under future thermal extremes, and demonstrating how warming can fragment thermal habitats. Future efforts should focus on TFE estimates at high temporal resolution and at regional to local river-reach scales, while incorporating species- and even population-specific dispersal. Our findings provide valuable perspectives for targeted monitoring and conservation efforts at both assemblage and species levels, offering key insights for future freshwater conservation strategies.

Online content

Any methods, additional references, Nature Portfolio reporting summaries, source data, extended data, supplementary information,

acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at <https://doi.org/10.1038/s41558-026-02731-9>.

References

- Barbarossa, V. et al. Threats of global warming to the world's freshwater fishes. *Nat. Commun.* **12**, 1701 (2021).
- Sayer, C. A. et al. One-quarter of freshwater fauna threatened with extinction. *Nature* **638**, 138–145 (2025).
- Déry, S. J., Martins, E. G., Owens, P. N. & Petticrew, E. L. Extreme hydrometeorological events induce abrupt and widespread freshwater temperature changes across the Pacific Northwest of North America. *Commun. Earth Environ.* **5**, 228 (2024).
- Scherer, L., Boom, H. A., Barbarossa, V. & van Bodegom, P. M. Climate change threats to the global functional diversity of freshwater fish. *Glob. Chang. Biol.* **29**, 3781–3793 (2023).
- Martínez-De León, G. & Thakur, M. P. Ecological debts induced by heat extremes. *Trends Ecol. Evol.* **39**, 1024–1034 (2024).
- Jørgensen, L. B., Ørsted, M., Malte, H., Wang, T. & Overgaard, J. Extreme escalation of heat failure rates in ectotherms with global warming. *Nature* **611**, 93–98 (2022).
- Biela, V. R. et al. Premature mortality observations among Alaska's Pacific salmon during record heat and drought in 2019. *Fisheries* **47**, 157–168 (2022).
- Till, A., Rypel, A. L., Bray, A. & Fey, S. B. Fish die-offs are concurrent with thermal extremes in north temperate lakes. *Nat. Clim. Change* **9**, 637–641 (2019).
- Ouellet, V., Mingelbier, M., Saint-Hilaire, A. & Morin, J. Frequency analysis as a tool for assessing adverse conditions during a massive fish kill in the St. Lawrence River, Canada. *Water Qual. Res. J.* **45**, 47–57 (2010).
- Murali, G., Iwamura, T., Meiri, S. & Roll, U. Future temperature extremes threaten land vertebrates. *Nature* **615**, 461–467 (2023).
- Pigot, A. L., Merow, C., Wilson, A. & Trisos, C. H. Abrupt expansion of climate change risks for species globally. *Nat. Ecol. Evol.* **7**, 1060–1071 (2023).
- Trisos, C. H., Merow, C. & Pigot, A. L. The projected timing of abrupt ecological disruption from climate change. *Nature* **580**, 496–501 (2020).

13. Meyer, A. S. et al. Temporal dynamics of climate change exposure and opportunities for global marine biodiversity. *Nat. Commun.* **15**, 5836 (2024).
14. Leal, C. G. et al. Integrated terrestrial-freshwater planning doubles conservation of tropical aquatic species. *Science* **121**, 117–121 (2020).
15. Mann, R. D. & Snow, C. G. Population-specific migration patterns of wild adult summer-run Chinook Salmon passing Wells Dam, Washington. *N. Am. J. Fish. Manag.* **38**, 377–392 (2018).
16. Venard, J. A. & Scarnecchia, D. L. Seasonally dependent movement of lake trout between two northern Idaho lakes. *N. Am. J. Fish. Manag.* **25**, 635–639 (2005).
17. Leroux, R., Pépino, M., Bordeleau, P. A., Bertolo, A. & Magnan, P. Animal movement in space and time: the role of thermal barriers and individual variation in modulating predator–prey overlap in stratified lakes. *Oikos* **2025**, e10528 (2025).
18. Rainville, V., Dupuch, A., Pépino, M. & Magnan, P. Intraspecific competition and temperature drive habitat-based resource polymorphism in brook charr, *Salvelinus fontinalis*. *Evol. Ecol.* **36**, 967–986 (2022).
19. Jones, L. A., Muhlfeld, C. C., Marshall, L. A., McGlynn, B. L. & Kershner, J. L. Estimating thermal regimes of bull trout and assessing the potential effects of climate warming on critical habitats. *River Res. Appl.* **30**, 204–216 (2014).
20. Snyder, C. D., Hitt, N. P. & Young, J. A. Accounting for groundwater in stream fish thermal habitat responses to climate change. *Ecol. Appl.* **25**, 1397–1419 (2015).
21. Antão, L. H. et al. Temperature-related biodiversity change across temperate marine and terrestrial systems. *Nat. Ecol. Evol.* **4**, 927–933 (2020).
22. Comte, L. & Olden, J. D. Climatic vulnerability of the world's freshwater and marine fishes. *Nat. Clim. Change* **7**, 718–722 (2017).
23. Earhart, M. L. et al. Identification of upper thermal thresholds during development in the endangered Nechako white sturgeon with management implications for a regulated river. *Conserv. Physiol.* **11**, coad032 (2023).
24. Di Cecco, G. J. & Gouhier, T. C. Increased spatial and temporal autocorrelation of temperature under climate change. *Sci. Rep.* **8**, 14850 (2018).
25. Duffy, K., Gouhier, T. C. & Ganguly, A. R. Climate-mediated shifts in temperature fluctuations promote extinction risk. *Nat. Clim. Change* **12**, 1037–1044 (2022).
26. Fleischmann, A. et al. Unprecedented social-ecological impacts of the 2023 extreme drought in the central Amazon. *Sci. Rep.* **15**, 41239 (2025).
27. Fleischmann, A. et al. Extreme warming of Amazon waters in a changing climate. *Science* **390**, 606–611 (2025).
28. Braz-Mota, S. & Luis Val, A. Fish mortality in the Amazonian drought of 2023: the role of experimental biology in our response to climate change. *J. Exp. Biol.* **227**, jeb247255 (2024).
29. Barbarossa, V. et al. Impacts of current and future large dams on the geographic range connectivity of freshwater fish worldwide. *Proc. Natl Acad. Sci. USA* **117**, 3648–3655 (2020).
30. Belletti, B. et al. More than one million barriers fragment Europe's rivers. *Nature* **588**, 436–441 (2020).
31. Huang, Z. & Wang, L. Angtze dams increasingly threaten the survival of the Chinese sturgeon. *Curr. Biol.* **28**, 3640–3647 (2018).
32. Chen, Q. et al. River damming impacts on fish habitat and associated conservation measures. *Rev. Geophys.* **61**, e2023RG000819 (2023).
33. Olden, J. D. & Naiman, R. J. Incorporating thermal regimes into environmental flows assessments: modifying dam operations to restore freshwater ecosystem integrity. *Freshw. Biol.* **55**, 86–107 (2010).
34. Bosmans, J. et al. FutureStreams, a global dataset of future streamflow and water temperature. *Sci. Data* **9**, 307 (2022).
35. Petsas, P., Doxa, A., Almpnidou, V. & Mazaris, A. D. Global patterns of sea surface climate connectivity for marine species. *Commun. Earth. Environ.* **3**, 240 (2022).
36. Senior, R. A., Hill, J. K. & Edwards, D. P. Global loss of climate connectivity in tropical forests. *Nat. Clim. Change* **9**, 623–626 (2019).
37. McGuire, J. L., Lawler, J. J., McRae, B. H., Nuñez, T. A. & Theobald, D. M. Achieving climate connectivity in a fragmented landscape. *Proc. Natl Acad. Sci. USA* **113**, 7195–7200 (2016).
38. Isaak, D. J. et al. Slow climate velocities of mountain streams portend their role as refugia for cold-water biodiversity. *Proc. Natl Acad. Sci. USA* **113**, 4374–4379 (2016).
39. Troia, M. J., Kaz, A. L., Niemeyer, J. C. & Giam, X. Species traits and reduced habitat suitability limit efficacy of climate change refugia in streams. *Nat. Ecol. Evol.* **3**, 1321–1330 (2019).
40. Brito-Morales, I. et al. Climate velocity can inform conservation in a warming world. *Trends Ecol. Evol.* **33**, 441–457 (2018).
41. Hoffmann, A. A. & Sgró, C. M. Climate change and evolutionary adaptation. *Nature* **470**, 479–485 (2011).
42. Stillman, J. H. Acclimation capacity underlies susceptibility to climate change. *Science* **301**, 65–65 (2003).
43. Comte, L. & Olden, J. D. Evidence for dispersal syndromes in freshwater fishes. *Proc. Biol. Sci.* **285**, 20172214 (2018).

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

© The Author(s) 2026

Methods

Species distribution data

We used the International Union for Conservation of Nature (IUCN) Red List of Threatened Species database, which provides EOO data for 11,552 extant fish species⁴⁴. We complemented IUCN EOO data by compiling point occurrence records from a combination of datasets (Supplementary Table 1). We followed the same procedure as IUCN—that is, we merged sub-basin units of the HydroBASINS datasets at level 8 containing one or more point occurrence records of the species⁴⁵. We included species with at least 10-point occurrence records available in the complementary dataset²⁹. Our analysis focuses on lotic species (that is, those that are found in flowing water bodies). Thus, we excluded lentic species that occur exclusively in stagnant water bodies²⁹. Species are lotic if they were associated with habitats containing at least one of the terms ‘river’, ‘stream’, ‘creek’, ‘canal’ or ‘channel’²⁹. We excluded species if their EOO areas were less than 10³ km² (>10 grid cells). Synonyms were collected from FishBase, IUCN and ref. 46, with accepted species names validated in FishBase. Our final dataset included 9,809 species. We compared species coverage derived from the integrated point-occurrence dataset with the freshwater fish database in ref. 46, compiled at the biogeographic realm scale. This comparison indicates broadly representative global coverage, although species richness in northern Asia remains underestimated (Extended Data Fig. 9).

Water temperature data

We used the global water temperature database, FutureStream, which provides weekly water temperature data at a 5-arcminute spatial resolution generated using global hydrological and water temperature models (PCR-GLOBWB, DynWat)³⁴. These models are driven by climate data from five general circulation models (GFDL-ESM2M, HadGEM2-ES, IPSL-CM5A-LR, MIROC-ESM-CHEM and NorESM1-M), each forced by four RCP emissions scenarios (RCP2.6, RCP4.5, RCP6.0 and RCP8.5) as part of the Coupled Model Intercomparison Project Phase 5³⁴. We used a global river network at 5-arcminute spatial resolution, upscaled from the MERIT-Hydro dataset, to provide topological information for grid cells, along with additional hydrologic attributes such as river length⁴⁷. We chose the MERIT-Hydro (1/12°) river network over the PCR-GLOBWB river-routing network for the analysis because, although both are at the same spatial resolution, MERIT-Hydro is derived from a high-accuracy, hydrologically corrected digital elevation model, ensuring more realistic flow paths and river connectivity. This level of topographic detail is critical for accurately capturing species’ habitat structure and dispersal pathways. In contrast, the PCR-GLOBWB routing network is optimized for hydrological modelling and may oversimplify river topologies and length, making it less suitable for species-level ecological analyses such as TFE. Nonetheless, we note that the choice of drainage network had a minimal impact on TFE, as TFE quantifies species-level climate-induced spatial heterogeneity of warming, rather than pinpointing the exact location of individual suboptimal temperature pixels (Extended Data Fig. 10).

We used high-resolution (1 km) August stream-temperature data for the 1:100,000-scale National Hydrography Dataset Plus, provided by the NorWeST project⁴⁸. Historical mean August water temperatures spanning 1993–2015 were used to establish the relationship between temperature differences and distance for defining TFE. We selected this regional monthly temperature dataset because it is the only high-resolution water temperature dataset available at the ~1 km river-reach scale, which allows for a more accurate representation of stream network topology and thermal heterogeneity.

Species-specific thresholds for extreme water temperature

We used maximum weekly water temperatures to represent one side of species-realized niche limits. Previous research has suggested that increases in maximum water temperature constitute a large threat

to freshwater fish than changes in minimum water temperature or extreme flow conditions under climate change¹. To assess climate change threats to freshwater fish, we focused on maximum rather than mean thermal conditions, as extreme temperatures are more decisive drivers of local extinctions and potential range contractions^{1,49}.

We quantified species-specific thresholds for maximum weekly water temperature based on the extant distribution of water temperatures within species EOOs, similar to previous studies^{1,10,12}. The long-term averaged species-specific weekly maximum temperature threshold was estimated in two steps¹. First, we estimated the annual maximum weekly water temperature during 1976–2005 and calculated the mean of the 30-year time-series data for each grid cell. We then overlaid the species’ EOOs with the long-term averaged weekly maximum temperature and considered the 97.5th percentile of the mean annual maximum weekly water temperature within the species’ EOOs as the species-specific thresholds. We used the percentiles rather than absolute maximum values to reduce the influence of uncertainties and outliers in the threshold definition¹. To remain more conservative and resistant to outliers in our estimates of species-specific thresholds, we used the 97.5th percentile instead of the more commonly used 95th or 99th percentile to define extreme events. A comparison between our species-specific thresholds and the critical thermal maxima reported in ref. 22 suggests both under- and overestimations, but overall reasonable agreement (mean bias = 9%; Pearson’s $r = 0.52$; Extended Data Fig. 6). Further comparisons with species-specific thresholds defined at the 95th and 99th percentiles are provided in Supplementary Text 4 and Supplementary Figs. 4 and 5.

Definition of thermal exposure characteristics

We describe thermal exposure characteristics from four perspectives: thermal exposure intensity, magnitude, abruptness and timing. First, we defined an extreme thermal event as a period during which a species is exposed to temperatures above its species-specific threshold for at least three consecutive weeks (Extended Data Fig. 1). Although the three-week period is arbitrary, studies on a limited set of species suggest that even single-day extreme thermal events can have substantial biological impacts¹⁰. Here a three-week duration is chosen to avoid classifying short, transient temperature spikes as ecologically meaningful extremes, as many freshwater fish can buffer short-term exposure through behavioural or physiological acclimation^{50,51}. Moreover, because our species-specific thresholds represent the 97.5th percentile of weekly temperatures within each species’ current ranges, reflecting upper realized thermal conditions rather than acute physiological limits (Extended Data Fig. 6), a multi-week exceedance better captures chronic deviations from each species’ present-day thermal niche. Nevertheless, we also repeated all analyses using 2-, 4- and 6-week duration thresholds, and the overall spatial and statistical patterns remained consistent (Supplementary Figs. 6–8). Since multiple extreme thermal events can occur within a single calendar year, we defined the annual thermal exposure intensity as the maximum temperature observed across all extreme thermal events within the year. The intensity of each extreme thermal event was calculated as the mean of the temperature differences between the species-specific threshold and the weekly water temperatures exceeding that threshold (Extended Data Fig. 1). To complement the short-term effects of extreme thermal exposure, we also quantified the duration and frequency of short-term extreme events. For each species and grid cell, we calculated the annual total number of weeks above the species-specific threshold (duration) in extreme thermal events and the number of extreme thermal events per year (frequency) (Supplementary Figs. 1 and 2). Together with intensity, these metrics reflect the overall severity of short-term thermal stress experienced by species (Supplementary Fig. 3).

To reflect the long-term effects of extreme water temperatures, we introduce the concept of long-term extreme thermal events. If a

species experiences at least one short-term extreme thermal event in each year of a 5-year window, we consider the species to be exposed to unprecedented temperatures for a long period. The median of the 5-year exposure period is then taken as the time at which a long-term extreme thermal event occurs. This running-window is applied consecutively across all 5-year periods during 2006–2099. For species that breed annually or near-annually, 5 years represents a considerable number of breeding seasons at temperatures beyond which these species have never been recorded¹². This definition does not assume that extreme thermal events coincide with or fully span the breeding season in all species or years, but instead captures chronic, multi-year thermal pressure acting across generations.

Thermal exposure magnitude, abruptness and timing are all calculated based on long-term extreme thermal events (Extended Data Fig. 2). We calculate the cumulative percentage of species in the assemblage that have experienced lasting extreme thermal events over the course of the twenty-first century. In our framework, once a species experiences a long-term extreme thermal exposure event, it is counted as exposed for all subsequent years within that assemblage. First, thermal exposure magnitude is defined as the maximum of the cumulative percentage of species in the assemblage under long-term thermal exposure. Second, the abruptness of exposure for an assemblage was calculated as the percentage of newly exposed species that occur in the decade of maximum exposure relative to the exposure magnitude. Third, we identified the exposure abruptness timing as the midpoint in the decade of maximum exposure. Abruptness and timing were calculated only for assemblages in which five or more species were exposed, to avoid idiosyncrasies due to small sample sizes^{12,52}. Species not exposed before the end of the twenty-first century were excluded from this calculation.

Definition of TFE

We introduce the concept of temperature distance ($L_{j,i,s}$, in kilometres) to represent the thermal cost for species s when travelling through river reach i within river segment j . A river reach is defined relative to the spatial resolution of the underlying water temperature dataset, representing the smallest unit to which a water temperature attribute is assigned. A river segment represents a dendritic network composed of a cluster of connected river reaches. The core idea behind temperature distance is to reflect the thermal cost species may encounter when moving through a river network under rising temperatures. Our assumption is that reaches where temperatures exceed species-specific thresholds function as thermal barriers and impose thermal costs, with higher exceedance corresponding to higher thermal cost. Previous analysis focusing on landscape climate connectivity has directly established a linear relationship between thermal cost and temperature difference by setting temperature distance weight as a constant^{37,53}. Here we used the space-for-time method to establish a relationship between temperature distance ($L_{j,i,s}$) and temperature difference along time ($L_{j,i,s}$, in °C) (Supplementary Text 5):

$$L_{j,i,s} = f(\Delta T_{\text{time}}) \quad (1)$$

To reflect the thermal cost for each species, ΔT_{time} is defined as the temperature difference between future scenarios ($T_{\text{scj},i,s}$) and species-specific threshold ($T_{\text{threshold},s}$), which represents thermal exposure intensity as defined in thermal exposure characteristics:

$$\begin{aligned} \Delta T_{\text{time}} &= T_{\text{scj},i,s} - T_{\text{threshold},s} \quad (T_{\text{scj},i,s} > T_{\text{threshold},s}); \\ \Delta T_{\text{time}} &= 0 \quad (T_{\text{scj},i,s} \leq T_{\text{threshold},s}) \end{aligned} \quad (2)$$

where $T_{\text{scj},i,s}$ is the temperature of river reach i within river segment j under future scenarios connected with the habitat of species s . Under the assumption of space-for-time, temporal thermal gradients (ΔT_{time}) are represented by the spatial thermal gradients, expressed as the

absolute temperature differences (ΔT) between river reaches i and m within the same river segment j (noted as T_i and T_m):

$$\Delta T = |T_i - T_m| \sim \Delta T_{\text{time}} \quad (3)$$

To present the relationship between temperature difference (ΔT) and river-reach distance between river reaches i and m within the river segment j ($D_j^{i,m}$), we used August stream-temperature data from the NorWeST project, which provides water temperature data at the river-reach scale with 1 km resolution. $D_j^{i,m}$ are computed as the cumulative river-reach length summed along the flow path (watercourse distances), using the geometric properties of the National Hydrography Dataset Plus network adopted by the NorWeST project. This high-resolution, regional vector-based river network allowed us to calibrate the parameters a and b :

$$\Delta T = a(D_j^{i,m})^b \quad (4)$$

The median ΔT between reaches i and m within segment j , along with their river-reach distance ($D_j^{i,m}$), was fitted using a non-linear power function. The resulting exponents were $a = 0.85$ and $b = 0.24$. The representativeness of the ΔT - D relationship and parameters uncertainty and sensitivity are discussed in Supplementary Text 6 (Supplementary Figs. 9–14).

Based on the space-for-time method, the temperature distance $L_{j,i,s}$ can be interpreted from river-reach distance $D_j^{i,m}$, and ΔT_{time} is represented as a thermal cost expressed in distance units ($L_{j,i,s}$). Due to the convex shape of the fitted function, temperature distance responds less sensitively to early-stage warming compared to later periods, making this approach more conservative than previous analyses^{37,53}.

An empirical dispersal kernel $k(L)$ defined as a probability density function was adopted to explain the probability of successful dispersal over a given distance⁵⁴:

$$k(L) = C \frac{p}{\pi u \left(1 + \frac{L^2}{u}\right)^{p+1}} \quad (5)$$

$$K(L \geq x) = \int_x^{\infty} k(L) \quad (6)$$

Here L represents the temperature distance ($L_{j,i,s}$) in kilometres, k is the empirical dispersal kernel and $p = 0.18$ and $u = 550$ are movement parameters provided in ref. 54 and validated using comprehensive empirical data on species distributions in the Mississippi River basin⁵⁵. The parameters in the dispersal kernel have also been applied in regions such as the Indian Peninsula, where species distribution data are insufficient for independent calibration⁵⁴. We further discuss the sensitivity of this parameter set and its ecological interpretation in Supplementary Text 7 and 8 (Supplementary Figs. 15–18) ($C = 320.57$ is determined numerically such that $K(x \geq 0) = 1$).

Note that the $K(L)$ does not vanish, even for long distance. Therefore, a threshold B_0 is considered to represent thermal block—that is, interactions of populations from the species are completely blocked when the probability is lower than B_0 . In this study, we set $B_0 = 0.1$ as the thermal block threshold to incorporate abrupt changes:

$$B_{j,i,s} = K_{j,i,s} \cdot B_{j,i,s} = 0 \quad (K_{j,i,s} < B_0) \quad (7)$$

where $K_{j,i,s}$ is the probability of species s going through the temperature distance $L_{j,i,s}$, and $B_{j,i,s}$ is the truncation of $K_{j,i,s}$ after considering B_0 . Blocking probability is defined as $1 - B_{j,i,s}$, representing the intensity of thermal exposure on a scale from 0 to 1. The sensitivity of B_0 is discussed in Supplementary Text 9 (Supplementary Figs. 19 and 20).

For each species s , TFE is developed based on ref. 1, by multiplying $B_{j,i,s}$ as a weight factor:

$$\text{TFE} = 1 - \frac{\sum_{i=1}^N \left(\sum_{j=1}^M B_{j,i,s} d_{j,i,s} \right)^2}{\sum_{i=1}^N \left(\sum_{j=1}^M d_{j,i,s} \right)^2} \quad (8)$$

where n and N are numbers of river segments within the geographic range of species s ; m and M are numbers of river reach within the segment i for species s and $d_{j,i,s}$ is the length of river reach.

Partitioning the causes of TFE change

The factors driving changes in TFE can be grouped into four categories based on whether suboptimal temperatures occur in the historical or future period, and whether the affected reaches lie inside or outside a species' EOO (Extended Data Fig. 4). First, we identified river reaches that already exhibited suboptimal temperatures during the historical period, representing habitats that are naturally thermally isolated. Second, we considered river reaches that will be suboptimal due to climate-driven temperature changes. Third, we distinguished suboptimal conditions occurring within a species' geographic range ('in EOO'). Finally, we accounted for suboptimal temperatures in reaches located outside of a species' range but connecting habitat patches ('out EOO').

To isolate the contribution of climate change to TFE (ΔTFE), we calculate the difference between TFE during 2006–2099 and the mean TFE from 1976 to 2005. We define $\Delta\text{TFE} > 20\%$ as indicative of high risk, as nearly 96% of species are projected to experience mean ΔTFE values during 2006–2035 below this level relative to the historical baseline (1976–2005) under the RCP2.6 scenario. To quantify the extra effect of TFE occurring in river reaches outside of EOO but connecting habitat patches (TFEout), we assume these reaches are always optimal and calculate the TFE based on this assumption (TFEin). The difference between TFE and TFEin is then used to estimate TFEout. We do not instead assume that reaches inside the EOO are always optimal to calculate TFEout, because reaches within the EOO are inherently the priority for conservation.

Our approach highlights the significance of managing river-reach temperatures outside species' current ranges, particularly during early periods of warming when temperatures within EOOs may still be suitable. Three representative species with potamodromous, resident and anadromous life-history strategies were selected to map their EOOs and illustrate how warming shifts thermal blocks that affect TFE and TFEin values (Extended Data Figs. 7 and 8 and Supplementary Text 2).

TFE trajectory classification

We adopted the classification framework proposed in ref. 56. Both linear and non-linear models were fitted to compare the resulting classifications of TFE trajectories. Four statistical models were applied to each time series. Linear models were categorized into two types: 'linear' ($a_1 \neq 0, a_2 = 0$) for those with a significant trend (p values < 0.05), and 'no-trend' ($a_1 = a_2 = 0$) for those without a significant trend. For non-linear modelling, we used a second-order polynomial model ($a_2 \neq 0$) to capture the non-linear shape of the trajectory over time^{56–58}, and a step model to identify 'abrupt' changes. All classification codes are provided in ref. 56.

According to the trajectory shape, the function f followed one of the following forms:

$$f(t) = a_2 t^2 + a_1 t + a_0 + \varepsilon(t) \quad (9)$$

$$f(t) = a_0 + \beta_0 I(t > e) + \varepsilon(t) \quad (10)$$

where a_0, a_1, a_2 and β_0 are coefficients of the models and e is the threshold parameter, with $I(t > e) = 1$ when $t > e$ and 0 otherwise.

We adjusted the interval size parameter ($\delta \in [0,1]$) governing directional classification from the default value of 0.5 to 0.3 for quadratic trajectories. This modification requires consistent slope signs within the midpoint ($X_m \pm 15\%$ of the series length, rather than $\pm 25\%$ previously) to classify trends as 'increase' or 'decrease'; otherwise, trends are classified as 'stable'. The original value of 0.5 for δ was designed to minimize the false detection of trends by using half of the time series to decide the change direction⁵⁸. However, this also requires trajectories to change quickly at the early stage, which could lead to the misclassification to 'stable concave' when the trajectory includes a prolonged stable period followed by a later, more pronounced increase—a pattern commonly seen in the TFE pattern under RCP8.5. By reducing the interval size to 0.3, the method becomes more sensitive to delayed accelerations and improves the detection of these characteristic TFE patterns. Meanwhile, it ensures that the trajectory direction remains constant for at least 65% of the total timespan, which we consider sufficient to capture its main direction.

Temporal autocorrelation

The temporal autocorrelation of TFE was quantified by calculating the spectral exponent. We performed spectral analysis using periodograms derived from fast Fourier transforms to assess the power associated with each frequency in the detrended TFE^{24,25}. The spectral exponent was calculated as the slope of the linear regression between the log-transformed power and the log-transformed frequency. A more negative slope indicates stronger temporal autocorrelation, meaning that the time series is primarily influenced by low-frequency variations.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

Species' geographical ranges are available from the websites listed in Supplementary Table 1. The critical thermal maximum data used for comparison with species-specific thresholds are available via figshare at <https://figshare.com/s/eca5d4c047e8c87172db?file=7618726> (ref. 22). The FutureStream model results are available from <https://public.yoda.uu.nl/geo/UU01/T7TVTQ.html> (ref. 34). The global river network and the consistent hydro-geomorphology parameters are available via Zenodo at <https://doi.org/10.5281/zenodo.6482906> (ref. 47). The high-resolution (1 km) August stream-temperature data from the NorWeST project are available at <https://research.fs.usda.gov/rmrs/projects/norwest#modeled-summer-stream-temperatures> (ref. 48).

Code availability

TFE trajectory classification code is available via GitHub at https://github.com/matpelissie/abrupt_shifts_ecological_timeseries_classification (ref. 56). The code that was used to calculate TFE is available on CodeOcean at <https://codeocean.com/capsule/9950681/tree>.

References

44. The IUCN Red List of Threatened Species (IUCN, 2023); <https://www.iucnredlist.org/>
45. Freshwater Species Mapping Standards for IUCN Red List Assessments Version 6 (IUCN, 2019); https://nc.iucnredlist.org/redlist/content/attachment_files/Freshwater_Mapping_Protocol.pdf
46. Tedesco, P. A. et al. A global database on freshwater fish species occurrence in drainage basins. *Sci. Data* **4**, 170141 (2017).
47. Munier, S. & Decharme, B. River network and hydro-geomorphological parameters at 1/12° resolution for global hydrological and climate studies. *Earth Syst. Sci. Data* **14**, 2239–2258 (2022).

48. Isaak, D. J. et al. The NorWeST summer stream temperature model and scenarios for the western US: a crowd-sourced database and new geospatial tools foster a user community and predict broad climate warming of rivers and streams. *Water Resour. Res.* **53**, 9181–9205 (2017).
49. Román-Palacios, C. & Wiens, J. J. Recent responses to climate change reveal the drivers of species extinction and survival. *Proc. Natl Acad. Sci. USA* **117**, 4211–4217 (2020).
50. Neubauer, P. & Andersen, K. H. Thermal performance of fish is explained by an interplay between physiology, behaviour and ecology. *Conserv. Physiol.* **7**, eoz025 (2019).
51. Amat-Trigo, F., Andreou, D., Gillingham, P. K. & Britton, J. R. Behavioural thermoregulation in cold-water freshwater fish: innate resilience to climate warming? *Fish Fish.* **24**, 187–195 (2023).
52. Liu, X. et al. Future increase in aridity drives abrupt biodiversity loss among terrestrial vertebrate species. *Earth's Future* **11**, e2022EF003162 (2023).
53. Nuñez, T. A. et al. Connectivity planning to address climate change. *Conserv. Biol.* **27**, 407–416 (2013).
54. Lynch, H. J. et al. How restructuring river connectivity changes freshwater fish biodiversity and biogeography. *Water Resour. Res.* **47**, W05531 (2011).
55. Muneeppeerakul, R. et al. Neutral metacommunity models predict fish diversity patterns in Mississippi-Missouri basin. *Nature* **453**, 220–222 (2008).
56. Péliissié, M., Devictor, V. & Dakos, V. A systematic approach for detecting abrupt shifts in ecological timeseries. *Biol. Conserv.* **290**, 110429 (2024).
57. Berdugo, M., Gaitan, J. J., Delgado-Baquerizo, M., Crowther, T. W. & Dakos, V. Prevalence and drivers of abrupt vegetation shifts in global drylands. *Proc. Natl Acad. Sci. USA* **119**, e2123393119 (2022).
58. Rigal, S., Devictor, V. & Dakos, V. A method for classifying and comparing non-linear trajectories of ecological variables. *Ecol. Indic.* **112**, 106113 (2020).
59. Beck, H. E. et al. High-resolution (1km) Köppen-Geiger maps for 1901–2099 based on constrained CMIP6 projections. *Sci. Data* **10**, 724 (2023).
60. Linke, S. et al. Global hydro-environmental sub-basin and river reach characteristics at high spatial resolution. *Sci. Data* **6**, 283 (2019).

Acknowledgements

We thank L. Brown from the University of Leeds and J. White from the University of Birmingham for their constructive comments during the

PhD thesis examination, which helped improve the thesis chapter from which this work was developed.

Author contributions

H.W., J.L. and M.K. conceived the study. H.W. conducted the analyses and drafted the paper under the supervision of M.K., J.H. and J.L. J.H. also contributed to the development of the final draft of the paper. P.C. contributed to the implementation of Dijkstra's algorithm and the identification of connected river segments. V.B., M.K., J.H., P.C. and J.L. contributed to data interpretation and provided substantial revisions to the paper.

Funding

We acknowledge funding from the National Natural Science Foundation of China (grant no. 42361144001), School of Geography and water@leeds at the University of Leeds, the 111 Project (grant no. D25014), the National Foreign Experts Program (Category S) (grant no. S20240116), the Henan Province Foreign Scientist Studio (grant no. GZS2024013) and research projects (254000510004). This work was carried out as part of the IAHS HELPING Working Group on 'Stepwise ecological restoration of watersheds' and on 'Acceptance of nature-based solutions and their implementation in guidelines'. It was also supported by the UNESCO-Chair on 'Stepwise ecological restoration of watersheds'. V.B. was supported by the CML Impact fund of Leiden University.

Competing interests

The authors declare no competing interests.

Additional information

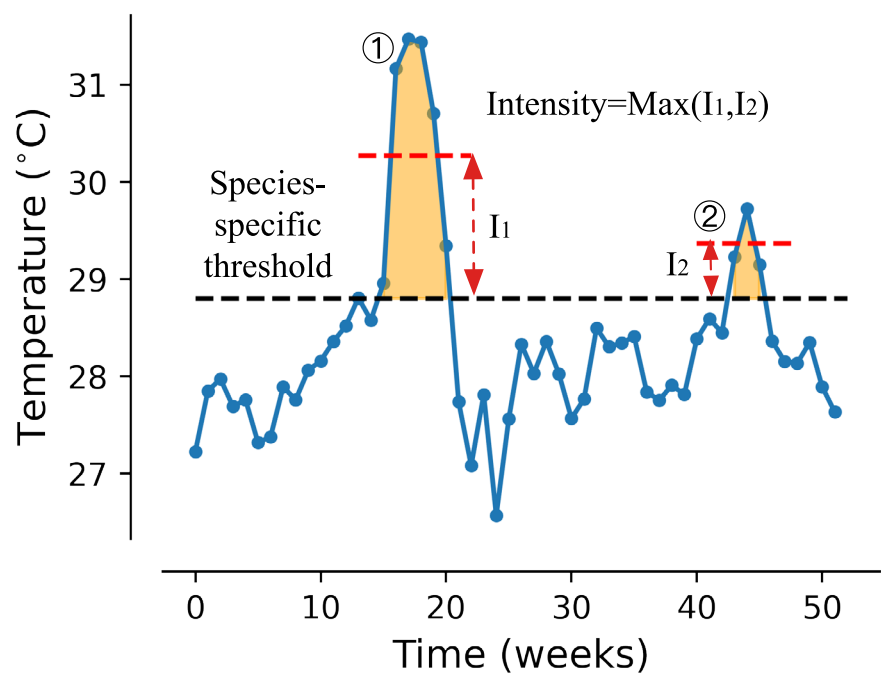
Extended data is available for this paper at <https://doi.org/10.1038/s41558-026-02731-9>.

Supplementary information The online version contains supplementary material available at <https://doi.org/10.1038/s41558-026-02731-9>.

Correspondence and requests for materials should be addressed to Junguo Liu.

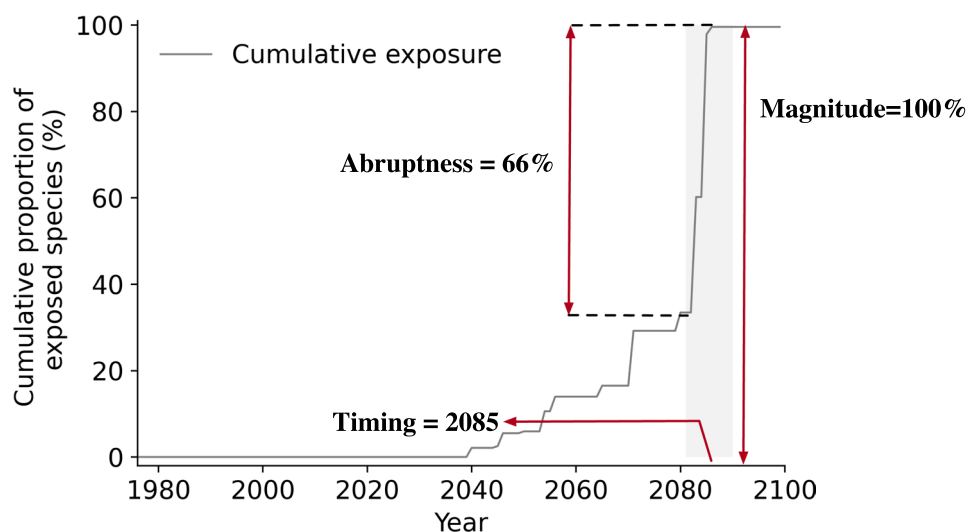
Peer review information *Nature Climate Change* thanks Gustavo Bizama, Paul A. Franklin and the other, anonymous, reviewer(s) for their contribution to the peer review of this work.

Reprints and permissions information is available at www.nature.com/reprints.



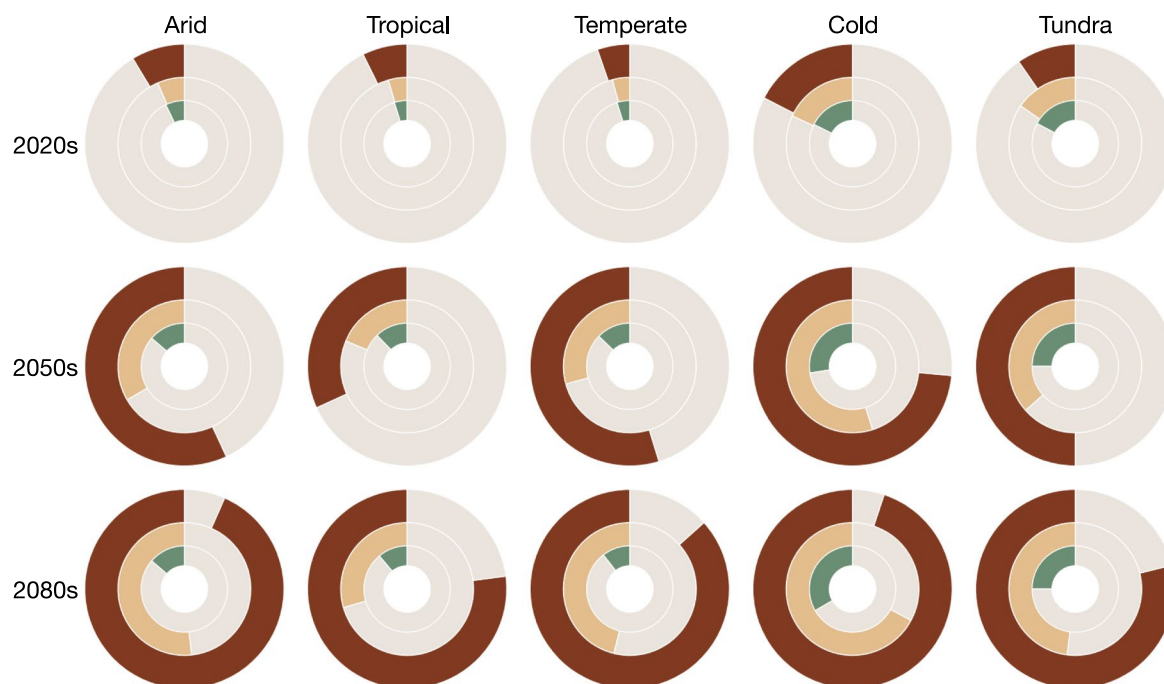
Extended Data Fig. 1 | Definition of metrics used for quantifying extreme thermal events within one calendar year. A thermal event (marked as ① and ②) is defined as when the average weekly water temperature (blue dotted line) is above the species-specific threshold (dashed black line) for more than three

consecutive weeks (yellow region). Intensity of a thermal event is defined as the mean temperatures of weeks above the species-specific threshold (I_1 and I_2). Annual thermal exposure intensity is defined as the maximum temperature observed across all extreme thermal events within the year.



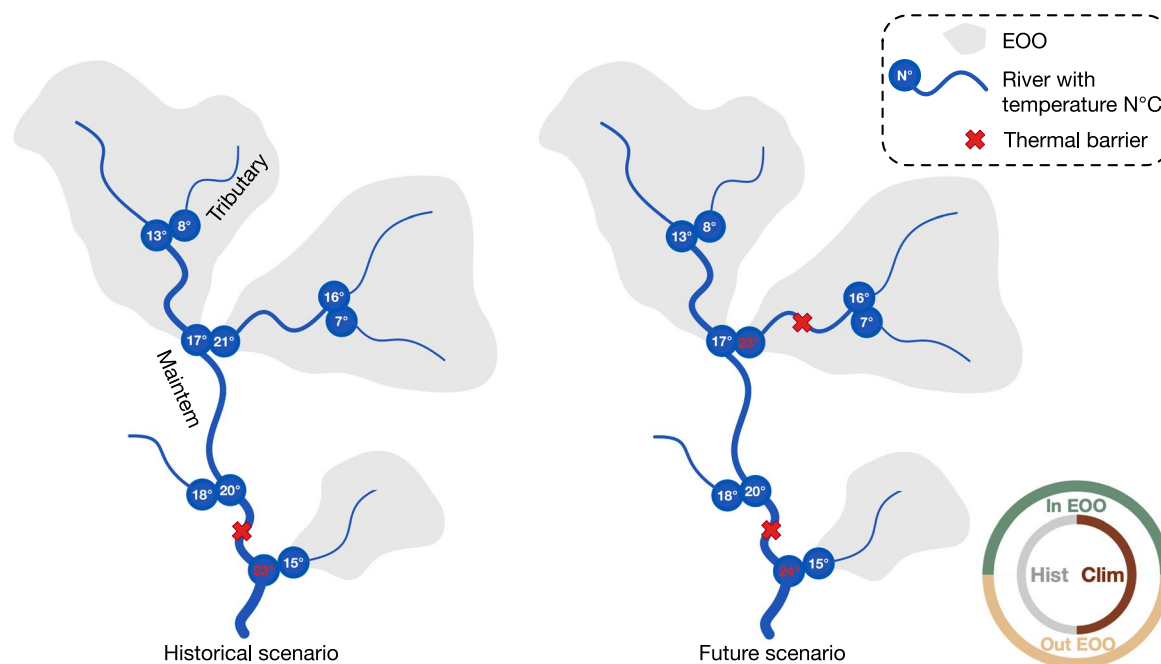
Extended Data Fig. 2 | Horizon profile and indicators (magnitude, abruptness, and timing) quantifying the long-term thermal exposure. Magnitude is defined as maximum of the cumulative percentage of species in the assemblage under long-term thermal exposure. Abruptness is defined as the percentage of

newly exposed species that occur in the decade of maximum exposure, scaled by the magnitude. Timing is calculated as the midpoint in the decade of maximum exposure.



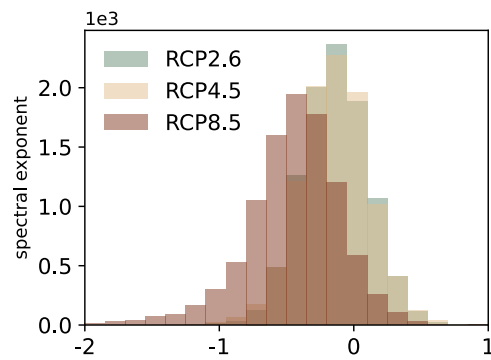
Extended Data Fig. 3 | Climate-zone stratification of species experiencing high thermal fragmentation exposure. Pie charts show the proportion of species experiencing high TFE caused by climate change ($\Delta\text{TFE} > 20\%$) during the 2020 s (2010–2039), 2050 s (2040–2069), and 2080 s (2070–2099). Columns represent the five major Köppen–Geiger climate zones³⁹ based on the

historical classification (1991–2020): arid, tropical, temperate, cold, and tundra. Concentric rings represent climate scenarios, from the inner to outer rings: RCP2.6, RCP4.5, RCP8.5. The numbers of species in each climate zone are 634 in arid, 6,501 in tropical, 2,214 in temperate, 408 in cold, and 52 in tundra regions.

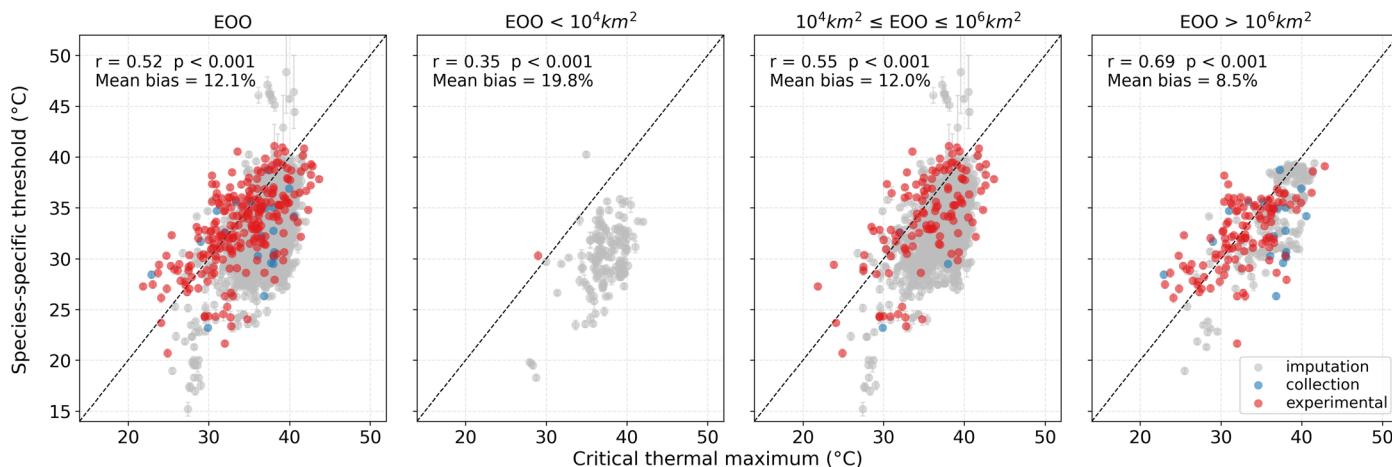


Extended Data Fig. 4 | Conceptual diagrams illustrating the causes of TFE change. In this example, the species-specific threshold is assumed as 22 °C. Under the historical scenario, a thermal barrier located outside the species' extent of occurrence (EOO) already imposes thermal fragmentation exposure (TFE). With future warming, an additional reach within the species' EOO exceeds

the threshold, creating a new internal thermal barrier. The labels on the right summarize the four categories of factors driving changes in TFE, defined by whether suboptimal temperatures occur in the historical (Hist) or future period (Clim) and whether the affected reaches lie inside (In EOO) or outside a species' EOO (Out EOO).

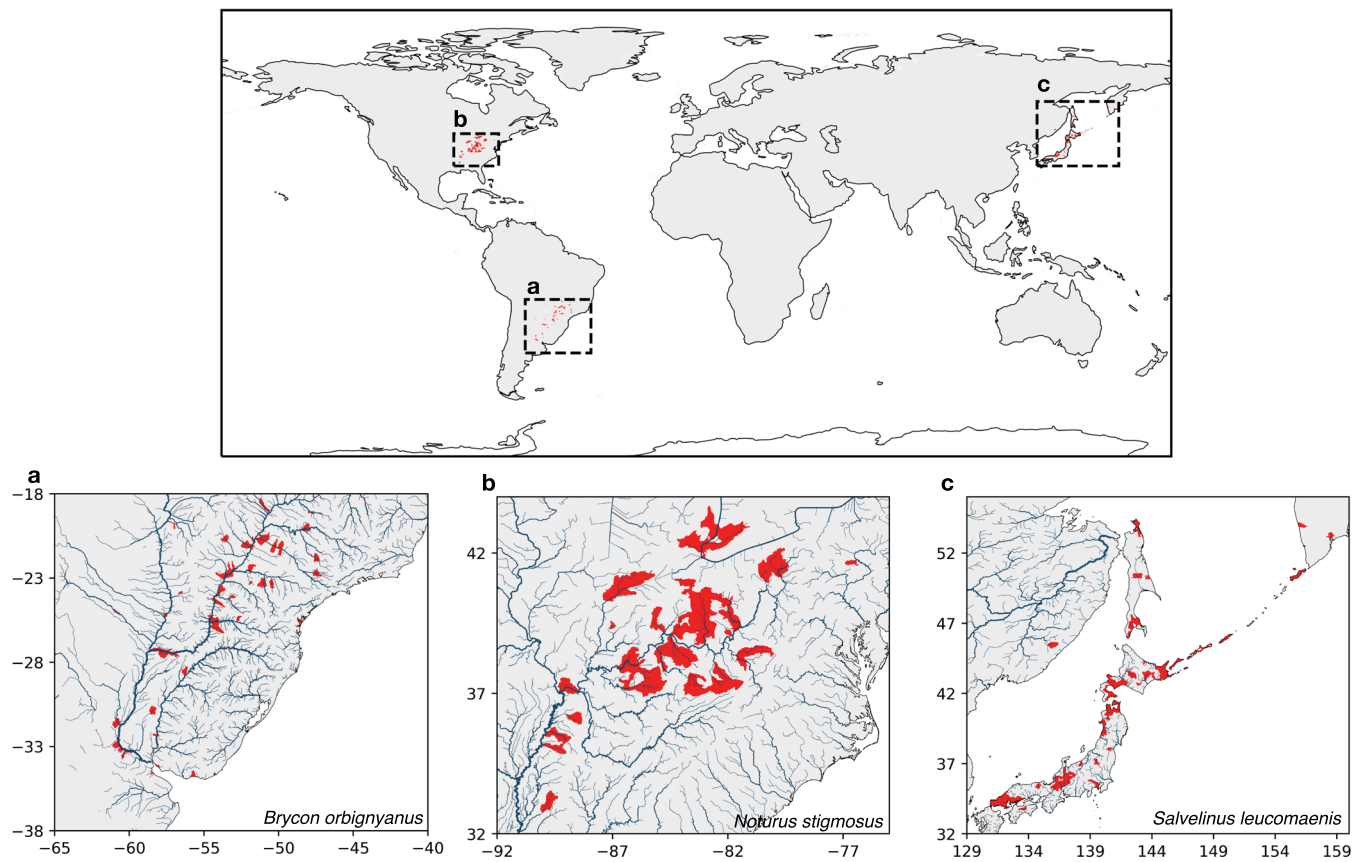


Extended Data Fig. 5 | Distribution of temporal autocorrelations of TFE under low (RCP2.6), intermediate (RCP4.5), and high (RCP8.5) emission scenarios. Temporal autocorrelations are quantified via the spectral exponent, with more negative values indicating greater autocorrelation.



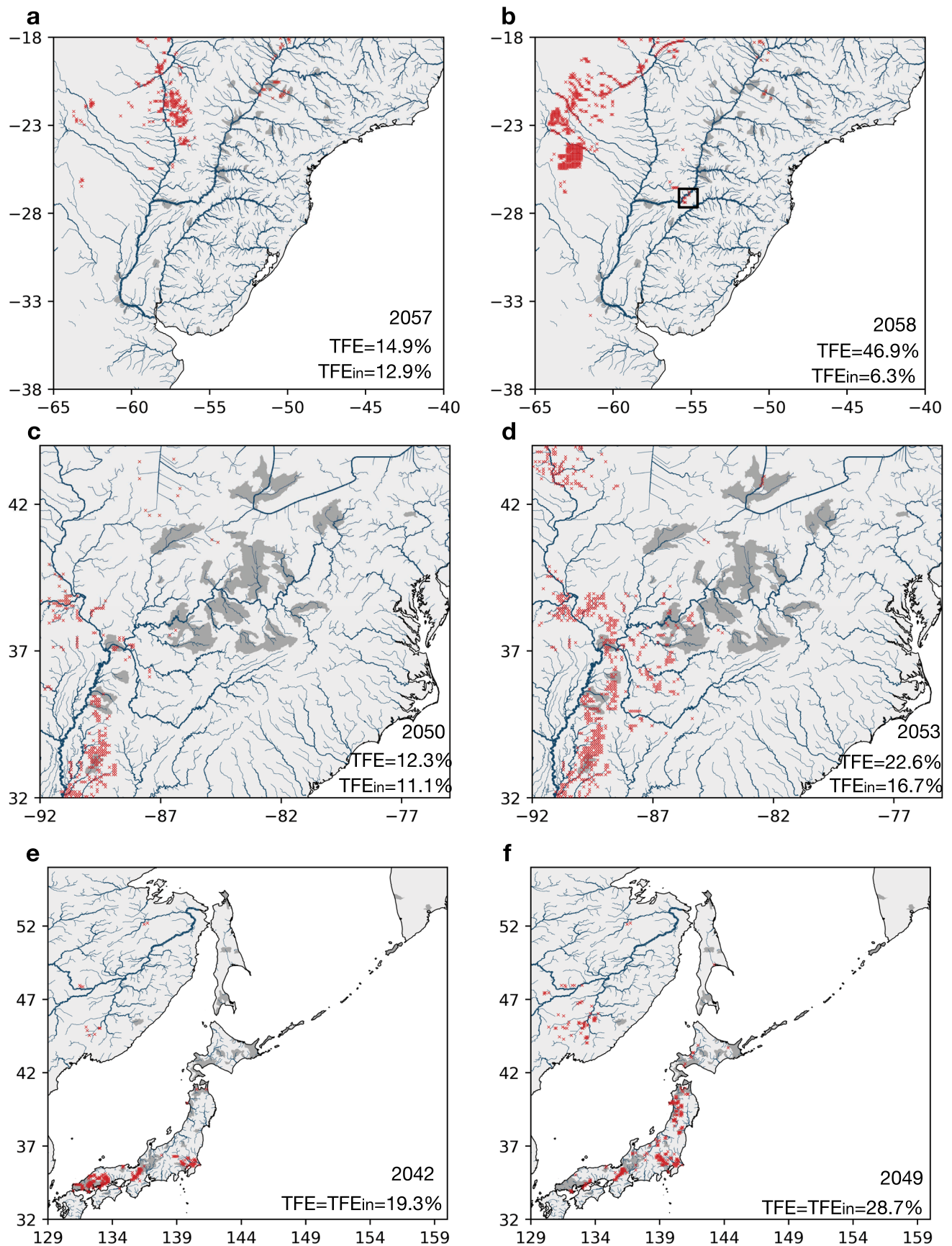
Extended Data Fig. 6 | Validation of range-based species-specific thermal thresholds against critical thermal maxima. Range-based species-specific thresholds were defined as the 97.5th percentile of weekly water temperature and compared against critical thermal maxima (CTmax) compiled by ref. 22, including laboratory-based, collection-derived, and imputed estimates for

1,799 freshwater fish species. The error bars represent standard deviations from five climate models, and the dots show the median values. Colors indicate CTmax data sources. Mean bias, Pearson correlation coefficients and two-sided unadjusted p -values are shown for all species combined and separately by species' extents of occurrence (EOO) area category.



Extended Data Fig. 7 | Global distributions of three representative freshwater fish species. Extent of occurrences are shown in red for *Brycon orbignyanus* (a), *Noturus stigmosus* (b), and *Salvelinus leucomaenis* (c), representing

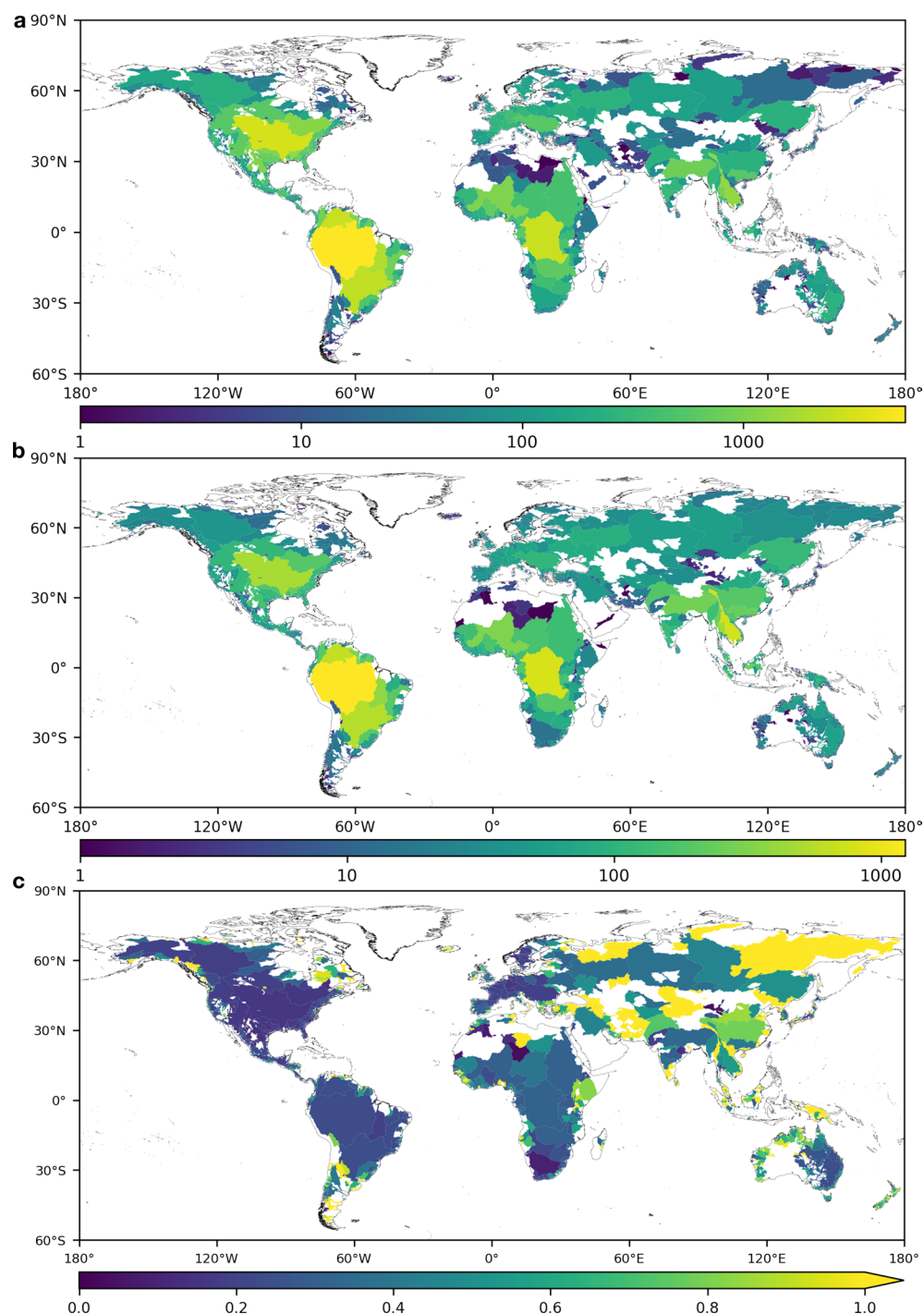
potamodromous, resident, and anadromous life-history strategies, respectively. Species distributions are shown at the global scale and overlaid with RiverATLAS⁶⁰ river reaches with discharge greater than $10 \text{ m}^3 \text{ s}^{-1}$.



Extended Data Fig. 8 | See next page for caption.

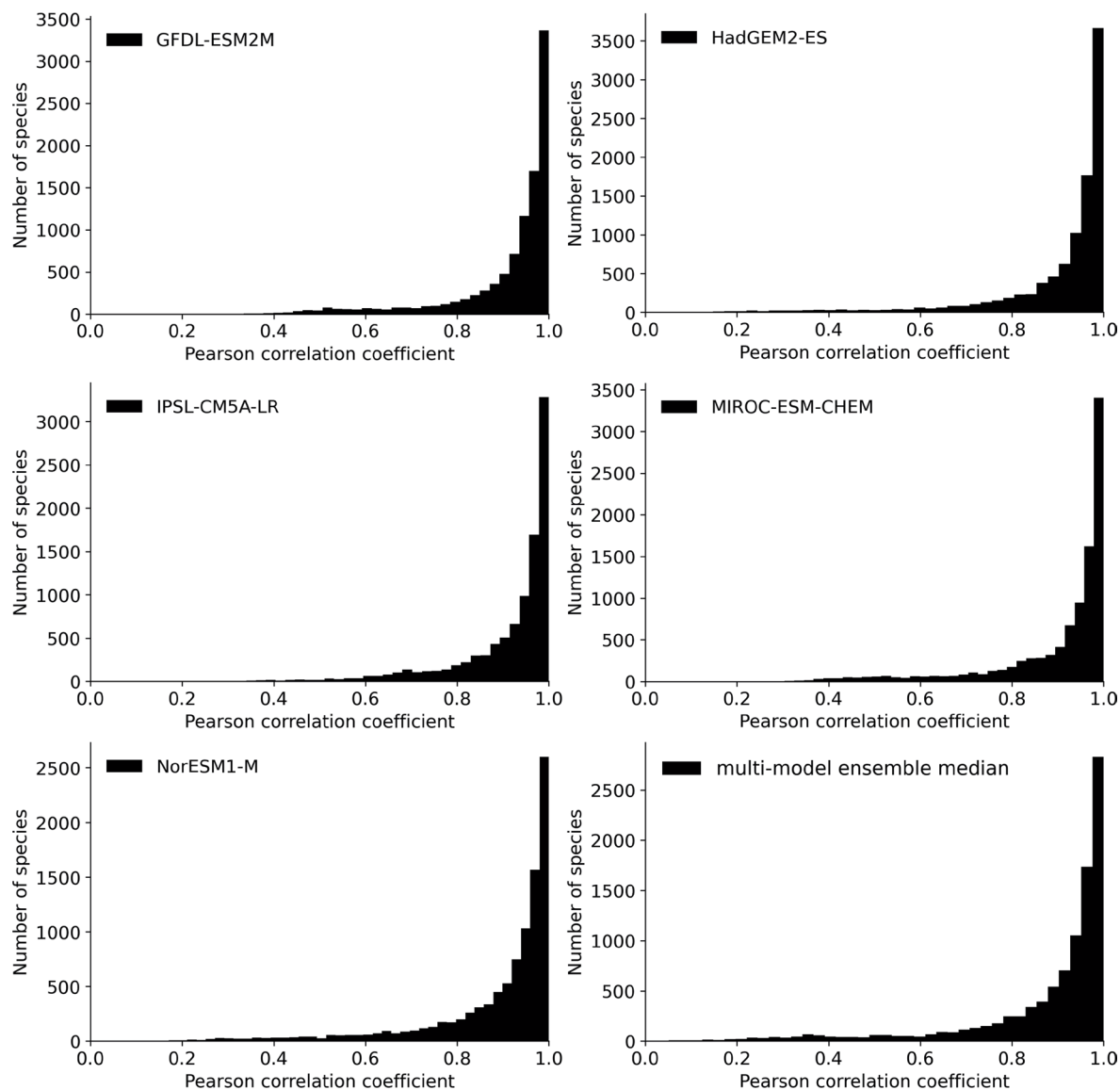
Extended Data Fig. 8 | Projected thermal blocks for three representative freshwater fish species. Projected distributions of thermal blocks are shown for *Brycon orbignyanus* (**a** and **b**), *Noturus stigmosus* (**c** and **d**), and *Salvelinus leucomaenis* (**e** and **f**) in two selected years under the NorESM1-M model with projected TFE and TFEin values labeled. Species extent of occurrences (EOOs)

are shown in grey and overlaid with thermal blocks (blocking probability > 0.9, red crosses) and rivers with discharge greater than $10 \text{ m}^3 \text{ s}^{-1}$ from RiverATLAS⁶⁰. The boxed region in panel **b** highlights thermal blocks outside the EOO of *Brycon orbignyanus* that nevertheless disrupt thermal connectivity among suitable habitats, explaining the difference between TFE and TFEin in 2058.



Extended Data Fig. 9 | Comparison of riverine freshwater fish species distributions. (a) Species distributions derived from the point-occurrence datasets compiled in this study to complement the IUCN data. (b) Riverine

freshwater species richness from ref. 46. (c) Ratio of species numbers between panels (b) and (a) (species count in (b) divided by that in (a)). All species occurrences are aggregated at the drainage-basin scale as defined by ref. 46.



Extended Data Fig. 10 | Sensitivity of TFE to river network data. Distributions of Pearson correlation coefficients are shown between detrended TFE from each of the five general circulation models (GFDL-ESM2M, HadGEM2-ES, IPSL-CM5A-LR, MIROC-ESM-CHEM and NorESM1-M) and the multi-model ensemble median

under RCP8.5. Correlations were calculated separately using river networks from MERIT-Hydro and PCR-GLOBWB. For the PCR-GLOBWB-based TFE, river length was derived directly from grid cell dimensions, with flow direction used to determine whether the zonal, meridional, or diagonal length was assigned.

Reporting Summary

Nature Portfolio wishes to improve the reproducibility of the work that we publish. This form provides structure for consistency and transparency in reporting. For further information on Nature Portfolio policies, see our [Editorial Policies](#) and the [Editorial Policy Checklist](#).

Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

- | | |
|-------------------------------------|--|
| n/a | Confirmed |
| ☐ | ☒ The exact sample size (<i>n</i>) for each experimental group/condition, given as a discrete number and unit of measurement |
| ☐ | ☒ A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly |
| ☐ | ☒ The statistical test(s) used AND whether they are one- or two-sided
<i>Only common tests should be described solely by name; describe more complex techniques in the Methods section.</i> |
| ☒ | ☐ A description of all covariates tested |
| ☐ | ☒ A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons |
| ☐ | ☒ A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals) |
| ☐ | ☒ For null hypothesis testing, the test statistic (e.g. <i>F</i> , <i>t</i> , <i>r</i>) with confidence intervals, effect sizes, degrees of freedom and <i>P</i> value noted
<i>Give P values as exact values whenever suitable.</i> |
| ☒ | ☐ For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings |
| ☒ | ☐ For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes |
| ☐ | ☒ Estimates of effect sizes (e.g. Cohen's <i>d</i> , Pearson's <i>r</i>), indicating how they were calculated |

Our web collection on [statistics for biologists](#) contains articles on many of the points above.

Software and code

Policy information about [availability of computer code](#)

Data collection	No code was used for the data collection in this study.
Data analysis	Custom Python scripts and Jupyter notebooks were developed to calculate thermal fragmentation exposure and are available in the Code Ocean capsule (https://codeocean.com/capsule/9950681/tree). Data processing were performed using Python v3.8.13. Packages include netcdf4 (1.7.2), numba(0.61.2), numpy (2.2.6), scipy (1.16.0), and xarray (2025.7.1). All data visualizations and map figures in this paper were created using Python with the cartopy (0.21.1), matplotlib (3.10.3), and geopandas (0.13.2). The map projections used is PlateCarree from cartopy. Coastlines and land features were rendered using cartopy's NaturalEarthFeature function, which sources data from the Natural Earth dataset. Trajectory classification was performed in R v4.2.1 using scripts based on the method described in https://github.com/matpelissie/abrupt_shifts_ecological_timeseries_classification .

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio [guidelines for submitting code & software](#) for further information.

Data

Policy information about [availability of data](#)

All manuscripts must include a [data availability statement](#). This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
- For clinical datasets or third party data, please ensure that the statement adheres to our [policy](#)

All datasets used in this study are publicly available, and the corresponding access links are provided in the Data Availability statement.

Research involving human participants, their data, or biological material

Policy information about studies with [human participants or human data](#). See also policy information about [sex, gender \(identity/presentation\), and sexual orientation](#) and [race, ethnicity and racism](#).

Reporting on sex and gender	This research does not involve human participants, their data, or biological material.
Reporting on race, ethnicity, or other socially relevant groupings	See above.
Population characteristics	See above.
Recruitment	See above.
Ethics oversight	See above.

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see [nature.com/documents/nr-reporting-summary-flat.pdf](https://www.nature.com/documents/nr-reporting-summary-flat.pdf)

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	Global assessment of freshwater fish exposures to future extreme thermal events
Research sample	Species geographic range data and weekly water temperature data from 1976 to 2099
Sampling strategy	We included all freshwater fish species with at least ten occurrence records in the source dataset. No statistical methods were used to predetermine sample size.
Data collection	Data were based on existing datasets and was collected online by the authors.
Timing and spatial scale	Global data since 1976 to 2099.
Data exclusions	Our analysis focused on lotic species, defined as species occurring in flowing water bodies. We therefore excluded lentic species that occur exclusively in stagnant water bodies. Species were classified as lotic if their habitat descriptions included at least one of the following terms: "river", "stream", "creek", "canal" or "channel". We also excluded species with extent-of-occurrence (EOO) areas smaller than 10 ³ km ² , corresponding to approximately ten grid cells (Barbarossa et al., 2020).
Reproducibility	This is not an experimental study, thus experimental replication was not performed.
Randomization	Not applicable.
Blinding	Not relevant, since this study is not experimental.

Did the study involve field work? ☐ Yes ☒ No

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology and archaeology
☒	☐ Animals and other organisms
☒	☐ Clinical data
☒	☐ Dual use research of concern
☒	☐ Plants

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging

Plants

Seed stocks	Not applicable.
Novel plant genotypes	Not applicable.
Authentication	Not applicable.