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Asymmetric impacts of climate change on thermal habitat suitability for inland lake fishes

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Climate change is altering the thermal habitats of freshwater fish species. We analyze modeled daily temperature profiles from 12,688 lakes in the US to track changes in thermal habitat of 60 lake fish species from different thermal guilds during 1980-2021. We quantify changes in each species' preferred days, defined as the number of days per year when a lake contains the species' preferred temperature. We find that cooler-water species are losing preferred days more rapidly than warmer-water species are gaining them. This asymmetric impact cannot be attributed to differences in geographic distribution among species; instead, it is linked to the seasonal dynamics of lake temperatures and increased thermal homogenization of the water column. The potential advantages of an increase in warmer-water species may not fully compensate for the losses in cooler-water species as warming continues, emphasizing the importance of mitigating climate change to support effective freshwater fisheries management.

Climate change is transforming habitats and species composition across diverse ecosystems[1–3]. Animals benefiting from the expansion of their preferred habitats often thrive as 'winners', whereas those losing preferred habitats within the same ecosystem become 'losers'[4–8]. Changes in thermal habitat are of particular concern for freshwater fish, which are ectothermic and often require specific thermal conditions[9]. In contrast to marine species which often shift latitudinally to seek suitable thermal conditions in response to warming[10–12], freshwater species are often constrained by the geographical limits of inland water bodies, such as natural lakes and reservoirs. This spatial limitation forces them to adapt in place to changes in their preferred thermal habitats.

Assessing changes in the thermal habitat of temperate lakes is challenging due to the complex impact of climate change on lake temperatures[13,14]. As global temperatures rise, the thermal conditions within temperate lakes experience varying degrees of change across different depths and seasons, shaped by distinct lake features like morphology and water clarity[15–19]. This variability complicates predictions of thermal habitat changes for resident fish species. Thermal habitat or fish abundance changes are often linked to single-depth temperature variations, typically at the surface, potentially overlooking thermal dynamics within lakes that affect fish populations[20–23]. While predicting changes in thermal habitats based on simulated lakes or projected climate scenarios has been extensively explored[24–28], relatively less attention has been given to retrospectively analyzing historical changes with what is considered more accurate temperature data from models that account for actual lakes and historical meteorological observations[29]. A thorough examination of historical data, capturing the entire vertical temperature profile of lakes, could refine our understanding of changes in fish thermal habitats, providing valuable insights into the evolving dynamics of thermal habitats and their implications for fish communities in freshwater ecosystems.

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While many metrics for assessing fish thermal habitat exist[30,31], this study focuses on one of the most relevant and widely available growth-related thermal metrics: final temperature preferendum. The final temperature preferendum, the temperature that fish gravitate toward in a thermal gradient, often closely matches the optimal growth temperature, the temperature at which growth is maximized under conditions of unlimited food availability[32]. The final temperature preferendum can be more readily determined in laboratory settings compared to the optimal growth temperature, offering more consistent results across a wider range of species[32]. This temperature is the one that fish would instinctively seek out in their natural environments, if not constrained by other environmental factors[33]. To gauge the availability of preferred thermal habitats over time, this study focuses on the number of days per year when a lake's temperature profile included the final temperature preferendum for each species (referred to as 'preferred days'). Changes in preferred days should be sufficiently sensitive to reflect whether the lakes' overall thermal habitats are moving towards or away from the species' optimum[34], as other metrics of natural lakes that influence thermal habitat availability are relatively stable (e.g., total size/volume of the lake).

In this work, we utilize three datasets to determine the preferred days for various fish species from three thermal guilds, each having distinct spatial ranges: (1) modeled daily temperature profiles of lakes, (2) geographic ranges of 60 freshwater fish species, and (3) final temperature preferenda for these species. The lake temperatures, spanning from 1980 to 2021, are estimated using the General Lake Model, covering 12,688 lakes in the midwestern United States[35]. For each lake within a species' range, we calculate the annual number of days when temperatures within the water column of a lake include each species' final temperature preferendum. We then compare the average annual number of these preferred days for each species during a recent period (2001–2021) against an earlier baseline period (1980–2000) to quantify changes in their thermal habitats. Further, we examine correlations between the spatial ranges of fish, seasonal temperature cycles of lakes, meteorological influences (i.e., wind speed), and lake characteristics (i.e., depth, water clarity, and stratification duration) with the dynamics of thermal habitat changes. Our findings show that cooler-water species are losing preferred days much faster than warmer-water species are gaining them, an asymmetric impact not explained by species' geographic distributions but rather by seasonal lake temperature dynamics and increased thermal homogenization of the water column. These results indicate that gains among warmer-water species may not fully offset substantial losses among cooler-water species as warming continues, offering valuable insights into the potential impacts of climate change on inland fish communities and providing important considerations for effective freshwater fisheries management.

Results

Changes in preferred days for lake fish among different thermal guilds

On average, species that prefer cooler temperatures lost preferred days while those that prefer warmer temperatures gained preferred days (Fig. 1). Specifically, species preferring temperatures below 20.5 °C experienced fewer days meeting their preferred temperature conditions in 2001–2021 compared to 1980–2000. Conversely, species preferring temperatures above 20.5 °C generally saw an increase in preferred days during the same period (Fig. 1). Notably, the decrease in preferred days for species experiencing a decline was more pronounced than the increase for those experiencing a rise, with an average reduction of 7.5 (±2.7 SD, where SD represents standard deviation) days per lake versus an average increase of 2.8 (±1.3 SD) days

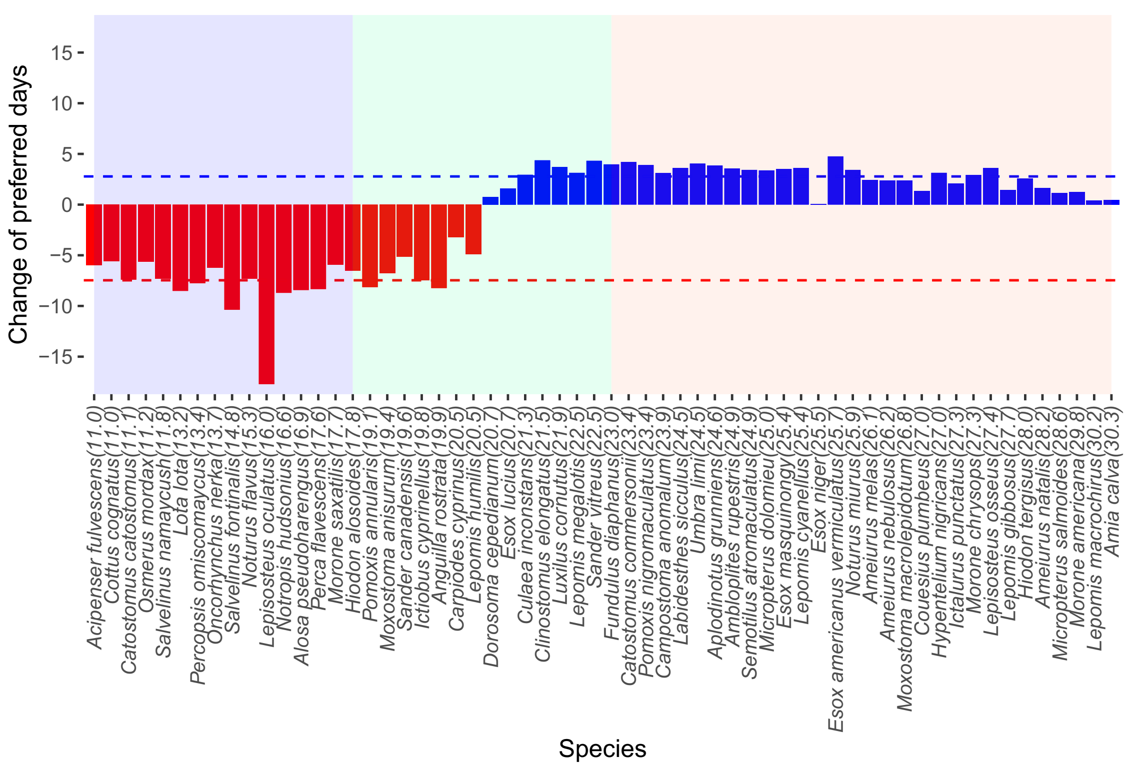

Fig. 1 | Change of species' averaged preferred days between 1980–2000 and 2001–2021. The numbers in parentheses on the x-axis indicate the final temperature preferendum of the corresponding species. Species are categorized by final temperature preferendum, with those below 19 °C classified as cold (blue shaded background), between 19 °C and 23 °C as cool (spring-green shaded background), and above 23 °C as warm (pink-orange shaded background). The dashed lines signify the average change for species that gained or lost days, respectively, with the blue line indicating the mean increase and the red line indicating the mean decrease in preferred days among species that gained or lost days, respectively. Source data are provided as a Source Data file.

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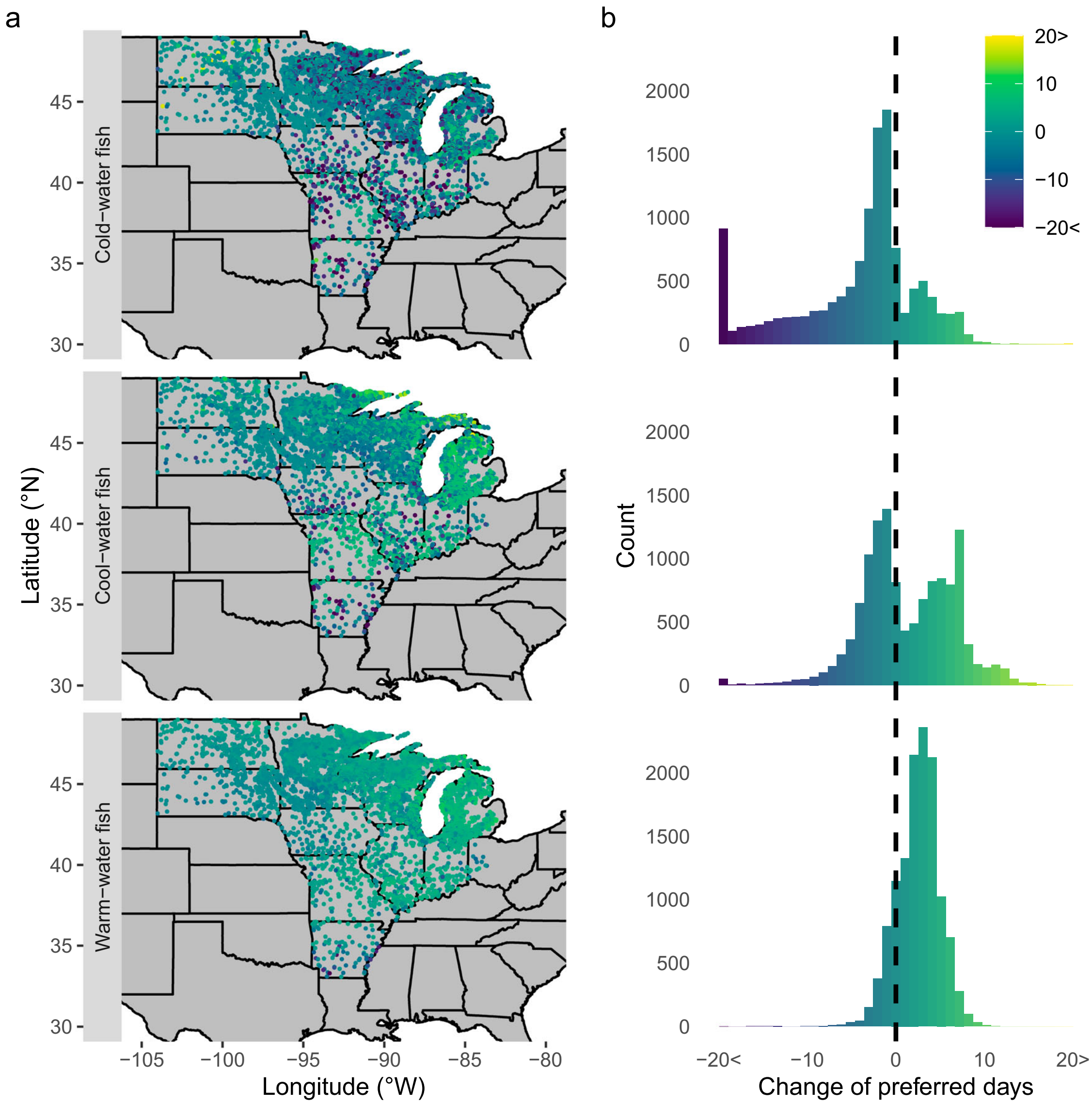

Fig. 2 | Spatial and frequency distribution of the change in average preferred days for cold-water (top), cool-water (middle), and warm-water (bottom) fish from 1980–2000 to 2001–2021. Each point in (**a**) represents the average change of days for all populations within the corresponding thermal guild. Histograms in (**b**) represent the count of lakes experiencing a specified change in preferred days. The color of the points in (**a**) and bars in (**b**) corresponds to the changes in preferred days as indicated by the color palette legend. Source data are provided as a Source Data file.

per lake (Fig. 1). Our analysis used a lake-days counting approach that treats all lake-days equally, regardless of lake size or the relative proportion of thermal habitat within each lake. Alternatively, basing the analysis on water volume would weigh larger lakes more heavily and take into account the greater water volume at shallower depths across all lakes. We reanalyzed the data based on habitat volume for a subset of lakes (4462, approximately 35%) for which hypsometry data was available. The results showed qualitatively similar outcomes: the asymmetric impact (i.e., big losses and small wins) on preferred habitat among thermal guilds persisted but was less pronounced (Supplementary Discussion and Supplementary Figs. 1a and 2a). In this region, cool-water species generally have a greater amount of preferred habitat compared to cold- and warm-water species, whether measured by volume or days (Supplementary Figs. 1b, 2b). Cold-water species experienced a proportionally larger habitat loss than the habitat gains observed for warm-water species (Supplementary Figs. 1b, 2b, and 3).

In this study, species are categorized based on their final temperature preferendum: those preferring temperatures below 19 °C are classified as cold-water species, those between 19 °C and 23 °C as cool-water species, and those above 23 °C as warm-water species[36,37]. The changes of preferred days for different thermal groups displayed distinct spatial patterns (Fig. 2a). Cold-water species experienced a widespread reduction in preferred days (Fig. 2). Results for cool-water species were bimodal, with relatively large increases in preferred days occurring in lakes within Michigan, northeastern Wisconsin, and northeastern Minnesota (Fig. 2). Warm-water species generally saw a mild rise in preferred days across most lakes (Fig. 2). Species-specific patterns generally matched the overall patterns of their thermal guild, despite notable differences in their spatial ranges (Supplementary Figs. 4–23).

Examining hypotheses for asymmetric thermal habitat change

To explore the potential causes of the observed asymmetry in thermal impacts on fish habitats, we evaluated three hypotheses: (1) The different geographic distributions of species within our study area drive the asymmetric impact, possibly with lakes containing cold-water species warming more rapidly than those hosting warm-water species; (2) The seasonal availabilities of preferred days vary by thermal guild. Specifically, the seasonal nature of lake temperatures restricts large increases in preferred days for warm-water species to only the hottest summer months, while cold-water species experience a reduction in their preferred days over a more prolonged duration throughout the year; (3) The coldest depth of the lake warms faster than the warmest, leading to a more marked reduction in preferred thermal habitat at the colder end of the temperature spectrum and a smaller increase at the warmer end.

Hypothesis one: differences in geographic ranges among species

Our first hypothesis regarding the asymmetric impact on preferred days concerns the influence of the geographic distribution of species. Because the calculated preferred days were restricted to lakes within a species' geographic range, different sets of lakes comprised the analysis for each species. This raises the possibility that lakes within the ranges of cold-water species might have warmed more rapidly, leading to a sharper decline in their preferred days. To test this hypothesis, we recalculated preferred days for each temperature point within the collective range of all cold-, cool-, and warm-water fish (i.e., spanning from 11 °C to 30 °C at 1-degree intervals) for every lake in our dataset. When disregarding species-specific spatial distributions, the same general pattern emerged: a more substantial reduction in the number of days featuring cooler-water temperatures, with an average of 6.9 and a standard deviation of 2.8, compared to a smaller increase in the number of days with warmer temperatures, averaging 2.3 with a standard deviation of 1.4 (Supplementary Fig. 24). This finding implies that the distinct geographical ranges of the species are not the underlying reason for the more marked decrease in cooler temperature days compared to the increase in warmer temperature days.

Hypothesis two: seasonal availabilities of preferred thermal habitats vary by thermal guilds

The second hypothesis investigated whether the seasonal dynamics of lake temperatures could explain the asymmetrical impacts on fish thermal habitats. We assessed the monthly changes in the number of days lakes contained the midpoint temperatures for cold-, cool-, and warm-water species (i.e., 15 °C, 21 °C, and 27 °C; referred to as cold-days, cool-days, and warm-days, respectively) for all lakes in the study area. A substantial reduction of cold-days occurred from May to August, with minor to moderate increases in March, April, and October (Fig. 3a). Cool-days declined in July and August, but this decline was compensated by increases in June and September (Fig. 3a). Large increases in warm-days were primarily limited to July (Fig. 3a). These monthly patterns are associated with the temperate seasonal temperature patterns and associated seasonal thermal scope of study lakes. Lake temperature ranges in this region was relatively narrow during colder months (e.g., from 0 °C to 4 °C for most lakes in January), but they expanded substantially in warmer months to encompass the preferred temperatures of all species (e.g., July; Fig. 3b). Cold-water species had a longer duration of preferred thermal habitat compared to warm-water species. Consequently, warming led to a reduction in the number of preferred days for cold-water species across several seasons (Fig. 3a). In contrast, warm-water species primarily experienced their preferred temperatures during a brief summer period, with climate warming significantly increasing their preferred days only during peak summer (Fig. 3c). Cool-water species saw both increases (in the shoulder seasons) and decreases (in the summer) in their preferred days, which tended to offset each other, resulting in minimal net changes (Fig. 3b). These monthly patterns support the notion that the seasonal nature of lake temperatures in temperate areas contributes to the observed asymmetry in thermal habitat changes.

Hypothesis 3: differential warming rates between the coldest and warmest depths of the lake

The third hypothesis scrutinized the trends of warming within lake temperature profiles by comparing the relative rates of increase in the lake's average highest and lowest temperatures. This analysis considered only days when lake temperature profiles ever fell within the thermal preference range of all studied species (11 °C–30.3 °C). The trends for the average highest and lowest temperatures were estimated using a linear model for each lake with temperature as the dependent variable and year as the independent variable (detailed methodology in the "Methods" section). A net gain pattern was identified if both trends were positive and the slope of the highest temperature was larger than that of the lowest temperature. This scenario suggests that the warmer end of the temperature spectrum expands more significantly than the loss at the cooler end, indicating an increase in thermal diversity within the lake (Fig. 4a). Conversely, a net loss pattern was identified if both trends were positive and the slope of the highest temperature was smaller than that of the lowest temperature. This implies that the temperature range lost at the cooler end outweighs gains at the warmer end, leading to a decrease in thermal diversity within the lake (Fig. 4b).

Our analysis revealed that most lakes (71%) exhibited the net loss pattern, with the lakes' coldest temperatures increasing at a faster rate than the lakes' warmest temperatures (Fig. 5a). The patterns were correlated with lake features like maximum depth and clarity. On average, net gain lakes had greater depths and lower clarity compared to net loss lakes (Fig. 5b, c). The duration of lake stratification also influenced thermal habitat changes, with lakes experiencing longer stratification periods more likely to exhibit the net gain pattern (Fig. 5d). Geographically, net gain lakes were predominantly located in Michigan, northeastern Wisconsin, and northeastern Minnesota, coinciding with the areas that experienced a substantial increase in preferred days for cool-water species (Figs. 2 and 5a). The results suggest that the dominant net loss pattern in lakes is likely a contributing factor to the observed asymmetry in thermal habitat changes.

Discussion

Climate warming has altered the thermal habitats of lake fish. This study highlights a significant asymmetry: species with lower thermal preferences experienced a more pronounced reduction in thermal habitat than the concomitant gain in thermal habitat for species that prefer warmer temperatures. After evaluating potential explanations for this pattern, we concluded that the asymmetric impact cannot be attributed to differences in the geographical ranges of the fish species. Instead, it relates to the seasonal dynamics of lake temperatures in temperate regions and a decreased diversity in thermal habitats across the water column in most lakes.

The response of lake temperature dynamics to climate change is complex and dependent on individual lake characteristics rather than just lake latitude[18,38–40]. For example, lake warming rates can vary widely within a region, with the most rapidly warming lakes being widely geographically distributed[15]. Our study also found that thermal habitat changes did not display clear latitudinal patterns (Fig. 2a). We examined a previously underexplored aspect of lake warming: the differential warming rates between a lake's average lowest and highest temperatures, which affect the net gain or net loss in fish thermal habitat diversity. Our analysis revealed that most lakes exhibited the net loss pattern, where the coldest portion of the lake warmed faster than the warmest. While the mechanisms driving this pattern are not fully understood, they may be related to factors such as stronger winds that enhance vertical mixing (Supplementary Fig. 5) or evaporative cooling of surface waters[41]. A lake's response to these factors is largely determined by its depth and clarity. Net gain lakes typically have greater depth, lower clarity, and longer stratification duration compared to net loss lakes (Fig. 5b–d). Shallower, clearer lakes are more prone to wind-induced mixing and vertical heat transport, making them more susceptible to breaking stratification than deeper, murkier lakes, thus promoting a more uniform heat distribution throughout

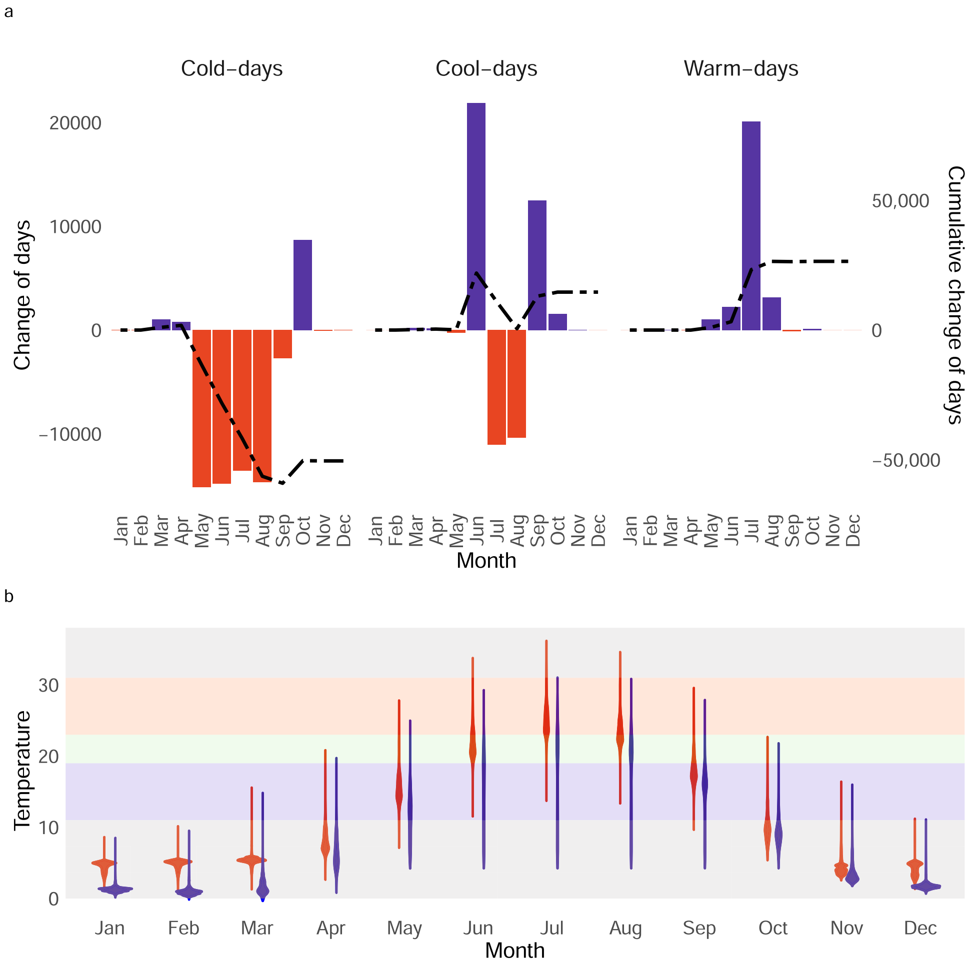

Fig. 3 | Monthly changes in days with specific lake temperatures and monthly average lake temperatures. In (**a**) monthly variation in average days with lake temperatures containing 15 °C, 21 °C, and 27 °C, the middle points of the preferred temperature range for cold/cool/warm-water species, between 1980–2000 and 2001–2021. The dashed lines, corresponding to the secondary axis on the right, represent the cumulative change of days. The value in each panel indicates the total annual change of days across all 12,688 lakes. In (**b**), violin plots represent the monthly average temperatures from 1980 to 2021 for each of the 12,688 lakes, with the red portions indicating the average highest temperatures and the blue portions indicating the average lowest temperatures of each lake. The width of the colored areas for each month is proportional to the frequency of the corresponding temperature across lakes. Species are categorized by final temperature preferendum, with those between 11 °C and 19 °C classified as cold (blue shaded background), between 19 °C and 23 °C as cool (spring-green shaded background), and between 23 °C and 30.3 °C as warm (pink-orange shaded background). Temperatures outside the 11 °C–30.3 °C range are shaded gray. Source data are provided as a Source Data file.

the water column[42]. Pilla et al. evaluated 102 relatively deep lakes globally and empirically confirmed that deep layers are warming more slowly than shallow layers within those lake[43], aligning with our observations in deep lakes (Fig. 5b).

Asymmetric patterns in thermal habitat change are associated with the seasonality of lake temperatures in north-temperate regions. Woolway[44] demonstrated that since 1980 the onset of spring and summer temperatures in Northern Hemisphere lakes has advanced, while the arrival of autumn has been delayed, leading to an extended summer season. These alterations are well known to affect fish reproductive success, which is highly sensitive to seasonal temperature cues[45]. Even subtle variations can lead to phenological mismatches, causing fish to spawn at suboptimal times and potentially reducing embryo hatch rates[46]. Our study highlights the direct impact of seasonal temperature changes on fish growth-related thermal habitats, yet the cascading effects could be more complex than what is revealed here. For instance, winter warming seems to have minimal direct impact on fish growth-related thermal habitat (Fig. 3a), as average winter temperatures remain much lower than the preferred temperatures of most fish species (Fig. 3b). However, in lakes with seasonal ice, the early thawing of ice caused by winter warming may lead to premature warming of lake waters, effectively advancing the onset of spring or prolonging summer season, which can influence the reproduction, survival, as well as growth of fish[47,48].

This study focused on the changes in the daily availability of thermal habitats across different species. However, these changes come with additional complexities that could intensify the asymmetric impacts. For instance, fish growth rates exhibit a modest rise with temperatures below the optimal point, yet experience a sharp decline when temperatures exceed this threshold (Fig. 6)[49]. Consequently, each preferred day lost by cooler-water species could have a more severe negative impact than the incremental benefits warmer-water species gain from an additional preferred day. Moreover, expanding thermal habitats for warmer-water species does not guarantee a rise in their growth rates, due to potential limitations from other factors. Also, cold temperatures are typically found in deep layers of the lake during the stratified season. With warming, the optimal temperatures for cooler-water species might shift even deeper[50], where they may encounter adverse conditions such as reduced oxygen levels[51], thus limiting their access to optimal

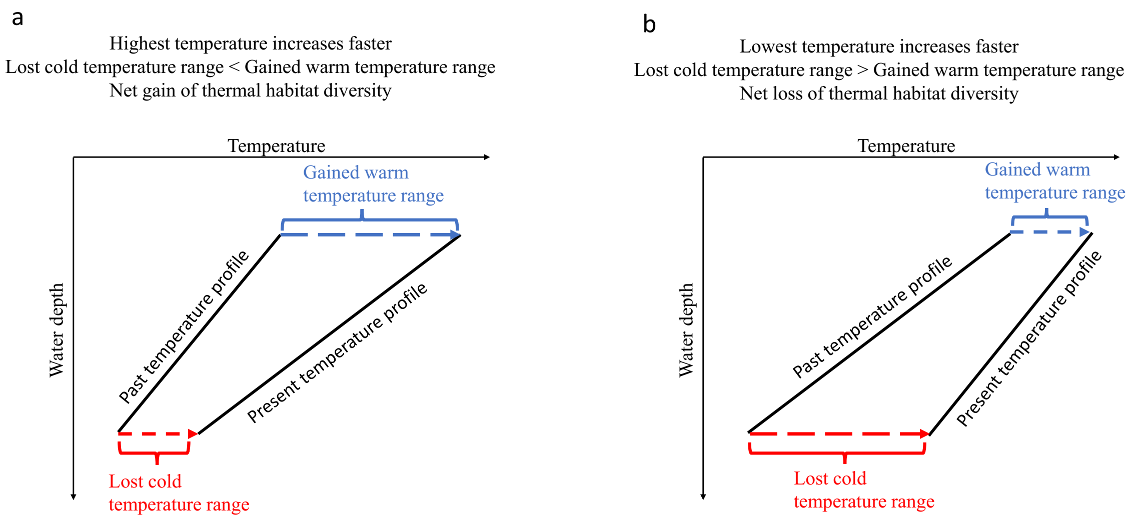

Fig. 4 | Two patterns of lake temperature profile shifts due to warming. The solid black lines represent the simplified temperature profiles: the left line represents the profile in the past, and the right line represents the current profile, which has shifted to warmer temperatures. The label "lost cold temperature range" indicates temperature ranges that were present in historical profiles but are absent in contemporary ones. Similarly, the label "gained warm temperature range" identifies temperature ranges that were historically absent but are now present in current profiles. **a** displays a temperature profile shift pattern where the highest temperature increases faster than the lowest temperature, resulting in a smaller lost low-temperature range compared to the gained high-temperature range, thus indicating a net gain in thermal diversity. **b** illustrates a shift pattern where the lowest temperature increases faster than the highest temperature, resulting in a larger lost low-temperature range compared to the gained high-temperature range, thereby indicating a net loss in thermal diversity.

temperatures. In addition, the greater loss of preferred thermal habitat for cold-water fishes is especially concerning as they generally have less preferred habitat available in this region to begin with (Supplementary Figs. 1b, 2b and 3).

Climate change has created winners and losers across various ecosystems due to habitat change[5–8]. Yet, the success of winners may not offset the losses of losers in maintaining high-quality ecosystem services. For instance, in terrestrial ecosystems, the growth of secondary vegetation does not make up for the loss of carbon sequestration in declining rainforests[52]. Similarly, fishing opportunities—a vital service provided by freshwater ecosystems—may face net losses as fish communities change, posing challenges for fishery managers. The Resist-Accept-Direct framework has emerged as a strategic tool for policymakers to manage changes in ecosystem services due to climate change, gaining particular traction in freshwater fishery management[53]. This approach involves intentionally directing fishing efforts from cooler- to warmer-water fish species, assuming that the latter will fare better under warming conditions. There are lakes where the rise of warmer-water species coincides with the decline of cooler-water species, which supports the implementation of directing strategy in those lakes[21,54]. However, on a broader scale, the overall reduction in fishing opportunities due to the decline of cooler-water species might not be fully offset by the increase in warmer-water species. This highlights the need for robust climate mitigation strategies to support effective freshwater fisheries management.

Methods

Lake temperature data

Lake daily temperature profiles were derived using the process-based General Lake Model[29], with temperature estimates provided at 0.5-meter depth intervals, applied to 12,688 lakes across 11 U.S. states (North Dakota, South Dakota, Iowa, Michigan, Indiana, Illinois, Wisconsin, Minnesota, Missouri, Arkansas, and Ohio) from January 1, 1980, to December 31, 2021. This model relies on lake-specific parameters including lake location specified by latitude, longitude, and elevation, the maximal depth (supplemented by detailed hypsographic data where accessible), the surface area, and the clarity of the water. Meteorological inputs, including daily, lake-specific shortwave radiation, longwave radiation, air temperature, relative humidity, wind speed, and precipitation, were sourced from the North American Land Data Assimilation System. The data are publicly available at Corson-Dosch et al.[35].

Fish spatial range data

The freshwater fish species selected for this study are those that do not exclusively inhabit river ecosystems. The ranges of fish species in this study were sourced from a variety of federal, state, museum, and university sources, as part of the National Fish Habitat Partnership (NFHP) project and supplemented by NatureServe data. Additional information was obtained from databases including Biodiversity Information Serving Our Nation (BISON), Multistate Aquatic Resources Information System (MARIS), and the Global Biodiversity Information Facility (GBIF), along with state fish books and primary literature. The data were consolidated into species-specific datasets at the eight-digit hydrologic unit code (HUC8) level, which represents, to our knowledge, the most detailed and comprehensive spatial information on species existence across a broad scale. These datasets are accessible from Daniel and Neilson[55].

Final temperature preferendum data

The final temperature preferendum refers to a precise temperature (measured as a point instead of a range) that fish generally favor, consistently gravitating toward the regions with such temperature in the presence of a varied temperature gradient. Our study utilizes the final temperature preferendum data for 60 fish species, which were previously assembled by Hasnain et al. [30].

Matching the lake location with the fish's spatial range

In this step, we match the lake locations with fish ranges by verifying if the centroid's longitude and latitude of the lake fall within the boundary of the fish spatial range for each species. Lakes whose centroid coordinates do not lie within the fish range will not be included in the thermal habitat analysis for that particular species.

Calculating the preferred days and their change

Species were categorized into cold, cool, or warm thermal groups based on final temperature preferendum thresholds of 19 °C and

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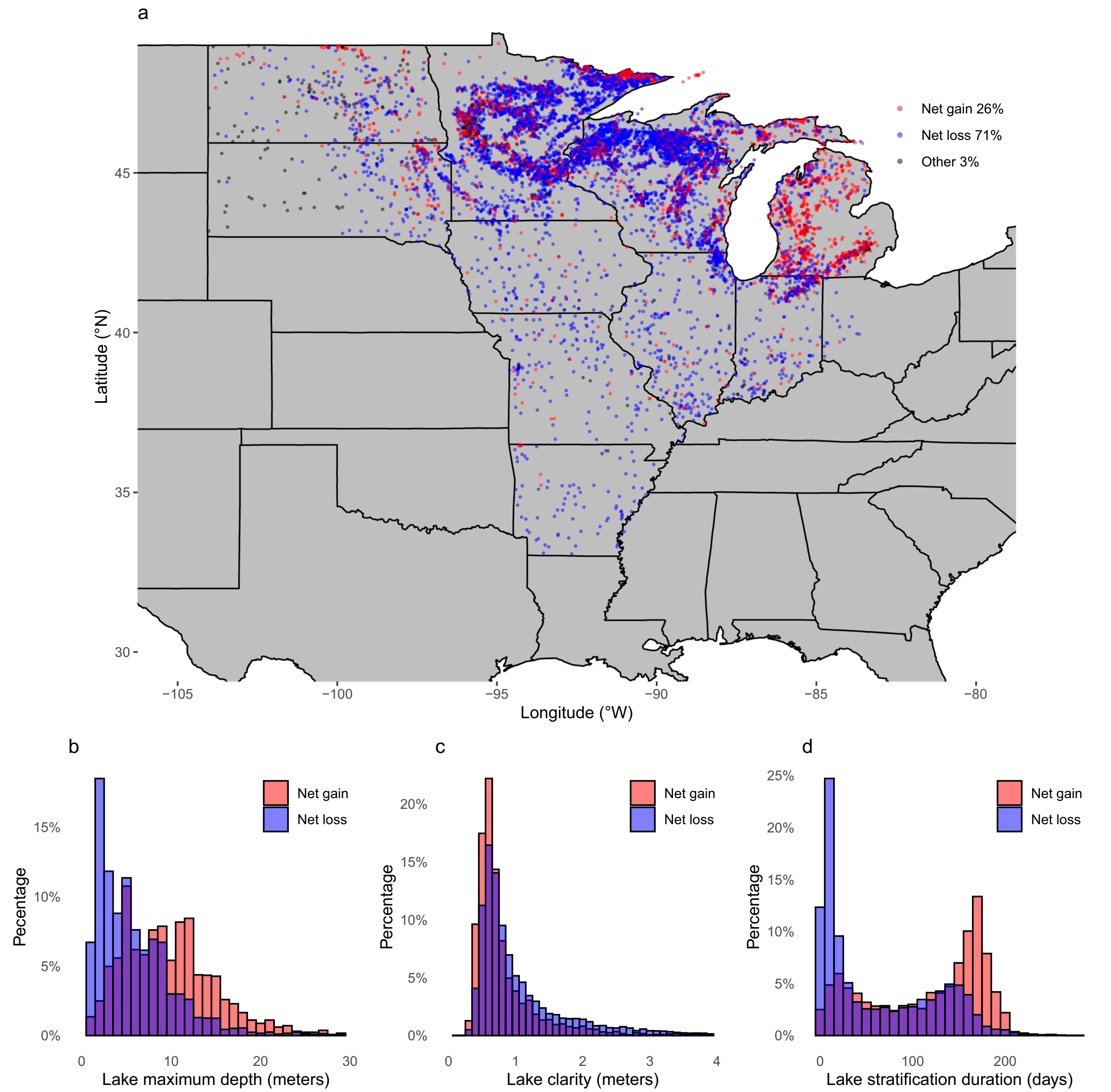

Fig. 5 | Spatial distribution of lake temperature shift patterns and their relationships with lake properties. **a** shows a map of lake temperature shift patterns across spatial locations. **b** presents a histogram of temperature shift patterns in relation to maximum lake depth. **c** presents a histogram of temperature shift patterns in relation to lake clarity. **d** presents a histogram of temperature shift patterns in relation to lake stratification duration. Source data are provided as a Source Data file.

23 °C[36,37]. For lakes within the species' spatial range boundaries, we calculate the number of days per year when the lake temperature profile includes the final temperature preferendum (preferred days) for each lake-species pair. To assess shifts in these preferred days, we calculate the difference in average preferred days between two time periods: a recent period (2001–2021) and an earlier baseline period (1980–2000).

Comparing changes in preferred days with changes in preferred volumes

Our analysis used a lake-days counting approach that treats all lake-days equally, regardless of lake size or the relative proportion of thermal habitat within each lake. Alternatively, when basing the analysis on water volume, larger lakes are weighted more heavily, and the greater water volume at shallower depths across all lakes is considered. We reanalyzed the data based on habitat volume for a subset of 4462 lakes (approximately 35%) that had available hypsometry data. Lake daily temperature profiles were measured at 0.5-meter depth intervals. The areas of identified layers containing the species' preferred temperatures were multiplied by 0.5 to calculate the preferred habitat volumes. To assess shifts in these volumes, we calculated the differences in average preferred volumes between two periods: a recent period (2001–2021) and an earlier baseline period (1980–2000). We then compared the changes in preferred days with

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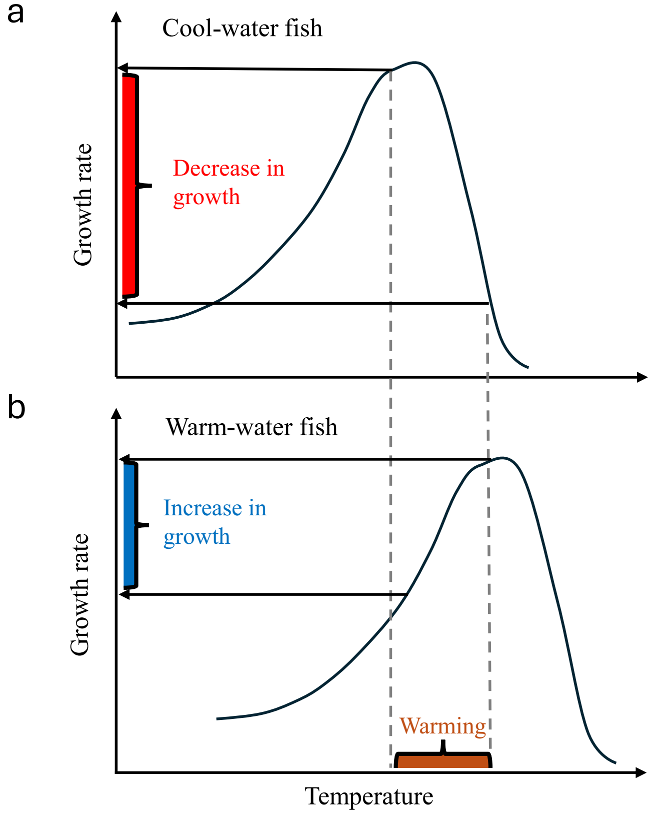

Fig. 6 | Fish growth rate in relation to water temperature. Fish growth rates experience a modest increase as temperatures approach the optimal point but undergo a sharp decline when temperatures exceed this threshold. Due to this asymmetry, the same degree of lake warming can result in a more pronounced decrease in the growth rates of cool-water species (**a**) compared to the increase in growth rates of warm-water species (**b**).

the changes in preferred volumes for the 4462 lakes with hypsometry information.

Examining three hypotheses for asymmetric thermal habitat change

To explore the potential causes of the observed asymmetry in thermal impacts on fish habitats, we proposed and scrutinized three hypotheses: (1) The geographic distribution of species plays a crucial role in driving the asymmetric impact, possibly with lakes containing cold-water species warming more rapidly than those hosting warm-water species; (2) Seasonal availability of preferred days varies by thermal guild. Specifically, the seasonal nature of lake temperatures limits large increases in preferred days for warm-water species to only the hottest summer month. In contrast, cold-water species face a reduction in their preferred days over a more prolonged duration throughout the year. Cool-water species experience comparable increases and decreases in preferred days in different months that may compensate for each other; or (3) The diversity of thermal habitats within the lake water column is reduced, as the increment in average minimum temperatures surpasses that of average maximum temperatures within a lake. Consequently, this leads to a more marked reduction at the colder end of the temperature spectrum and a smaller increase at the warmer end.

The difference in the species geographic distribution

Our first hypothesis regarding the asymmetric impact on preferred days concerns the influence of the geographic distribution of species. Because the calculated preferred days were restricted to lakes within a species' geographic range, a different set of lakes comprised the analysis for each species. This raises the possibility that lakes within the ranges of cold-water species might have warmed more rapidly, leading to a sharper decline in their preferred days. To test this hypothesis, we recalculated the preferred days for each temperature point within the collective range of all cold, cool, and warm-water fish (spanning 11 °C–30 °C at 1-degree intervals) across every lake in our dataset, without considering species-specific geographic distributions. By comparing the changes in preferred days across all lakes versus those specific to lake-species pairs, we sought to determine whether variations in species' spatial ranges contribute to the observed asymmetric pattern of changes in preferred days across different species. If disregarding the geographic distributions of species still yields a pattern where lakes generally show a greater reduction in days with cooler temperatures and a smaller increase in days with warmer temperatures, it would indicate that the asymmetric impact is not driven by the differences in the geographic distribution of the species.

Seasonal lake temperature patterns and seasonal availability of preferred thermal habitat

The second hypothesis examined whether the seasonal dynamics of lake temperatures could explain the asymmetrical impacts on fish thermal habitats. We calculated monthly changes in the number of days each lake contained temperatures of 15 °C, 21 °C, and 27 °C between early and later 21-year periods for all 12,688 lakes in the study area. These temperatures correspond to the midpoints of the temperature ranges for cold-, cool-, and warm-water species. To understand the seasonal availability of preferred thermal habitats for species from different thermal guilds, we also computed the monthly averages of the highest and lowest temperatures for each lake from 1980 to 2021 and compared them with the preferred temperature for species from different thermal guilds.

'Net loss' and 'net gain' in thermal habitat diversity

The third hypothesis examined the trends of warming in lake temperature profiles, classified by the relative rates of increase in a lake's average highest and lowest temperatures. This analysis considered only days when lake temperature profiles ever fell within the collective thermal preference range of all studied species (11 °C–30.3 °C). We identified specific dates during which the lake temperature profiles aligned with the collective preferred thermal range of the species, between 11 °C and 30.3 °C. A date qualifies if, for any given year between 1980 and 2021, the lake's daily maximum and minimum temperatures for that day fall between 11 °C and 30.3 °C. This step is to exclude those dates (mostly wintertime) when the temperature profile never falls within the range of 11 °C–30.3 °C, so that temperature change has no direct impact on the change of preferred days.

Subsequently, we computed the yearly averages of both the highest and lowest temperatures for each lake, using only the dates that met our criteria. The trends for the average highest and lowest temperatures were estimated using a linear model for each lake with temperature being the dependent variable and year as the independent variable.

A net gain pattern was identified if both trends were positive, with the highest temperature trend being greater. Conversely, a net loss pattern was identified if both trends were positive but the highest temperature trend was lower. If either trend was negative, the pattern was classified as other patterns.

Lakes where the annual average of highest temperatures increased more rapidly than its lowest temperatures would experience a more profound expansion of the temperature spectrum at the warmer end compared to the loss at the cooler end. This reflects a weaker overall lake temperature mixture and hence a net gain of thermal diversity (Fig. 4a). Conversely, if the annual average of lowest temperatures in a lake increased at a faster rate than the highest temperatures, the temperatures lost at the cooler end outweigh gains at the warmer end. This reflects a stronger overall lake temperature mixture and hence a net loss of thermal diversity.

Additionally, we explored the temporal trend of wind speed as stronger winds can contribute to stronger overall lake temperature mixing. The same dates as identified above for calculating the average highest and lowest temperature were selected to calculate the average wind speed. The trends for wind speed were estimated using a linear model for each lake with average wind speed being the dependent variable and year as the independent variable. We also compare the percentage distributions of net gain and net loss patterns in lake maximum depth, lake clarity, and the average annual lake stratification duration.

Reporting summary

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

Data availability

All data used in this study are publicly available and freely accessible. The large dataset (over 100 GB) containing daily lake temperature profiles and fish spatial range data can be downloaded from [https://www.sciencebase.gov/catalog/item/6206d3c2d34ec05caca53071] and [https://www.usgs.gov/data/native-ranges-freshwater-fishes-north-america], respectively, with details provided in the Methods section. Additional data are stored on GitHub (https://github.com/xucamel/Lake_thermal_habitat) and archived on Zenodo with the https://doi.org/10.5281/zenodo.14018961. Source data are provided as a Source Data file. Source data are provided with this paper.

Code availability

All analyses were conducted using the statistical software R version 4.3.2 (https://www.R-project.org/). The R code for this analysis is available on GitHub (https://github.com/xucamel/Lake_thermal_habitat) and has also been archived on Zenodo with the https://doi.org/10.5281/zenodo.14018961.

References

1. Nolan, C. et al. Past and future global transformation of terrestrial ecosystems under climate change. *Science* **361**, 920–923 (2018).
2. Pacifici, M. et al. Assessing species vulnerability to climate change. *Nat. Clim. Chang.* **5**, 215–225 (2015).
3. Pecl, G. T. et al. Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science* **355**, eaai9214 (2017).
4. Free, C. M. et al. Impacts of historical warming on marine fisheries production. *Science* **363**, 979–983 (2019).
5. Fulton, E. A. Interesting times: winners, losers, and system shifts under climate change around Australia. *ICES J. Mar. Sci.* **68**, 1329–1342 (2011).
6. Jackson, H. M. et al. Climate change winners and losers among North American bumblebees. *Biol. Lett.* **18**, 20210551 (2022).
7. Kafash, A. et al. Climate change produces winners and losers: differential responses of amphibians in mountain forests of the Near East. *Glob. Ecol. Conserv.* **16**, e00471 (2018).
8. Roeder, K. A., Bujan, J., de Beurs, K. M., Weiser, M. D. & Kaspari, M. Thermal traits predict the winners and losers under climate change: an example from North American ant communities. *Ecosphere* **12**, e03645 (2021).
9. Jutfelt, F. Metabolic adaptation to warm water in fish. *Funct. Ecol.* **34**, 1138–1141 (2020).
10. Dahms, C. & Killen, S. S. Temperature change effects on marine fish range shifts: A meta-analysis of ecological and methodological predictors. *Glob. Chang. Biol.* **29**, 4459–4479 (2023).
11. Perry, A. L., Low, P. J., Ellis, J. R. & Reynolds, J. D. Ecology: climate change and distribution shifts in marine fishes. *Science* **308**, 1912–1915 (2005).
12. Sunday, J. M., Bates, A. E. & Dulvy, N. K. Thermal tolerance and the global redistribution of animals. *Nat. Clim. Chang.* **2**, 686–690 (2012).
13. Kraemer, B. M. et al. Climate change drives widespread shifts in lake thermal habitat. *Nat. Clim. Chang.* **11**, 521–529 (2021).
14. Woolway, R. I. et al. Global lake responses to climate change. *Nat. Rev. Earth Environ.* **1**, 388–403 (2020).
15. O'Reilly, C. M. et al. Rapid and highly variable warming of lake surface waters around the globe. *Geophys. Res. Lett.* **42**, 1–9 (2015).
16. Pilla, R. M. et al. Deeper waters are changing less consistently than surface waters in a global analysis of 102 lakes. *Sci. Rep.* **10**, 1–15 (2020).
17. Rose, K. C., Winslow, L. A., Read, J. S. & Hansen, G. J. A. Climate-induced warming of lakes can be either amplified or suppressed by trends in water clarity. *Limnol. Oceanogr. Lett.* **1**, 44–53 (2016).
18. Winslow, L. A., Read, J. S., Hansen, G. J. A. & Hanson, P. C. Small lakes show muted climate change signal in deepwater temperatures. *Geophys. Res. Lett.* **42**, 355–361 (2015).
19. Winslow, L. A., Read, J. S., Hansen, G. J. A., Rose, K. C. & Robertson, D. M. Seasonality of change: Summer warming rates do not fully represent effects of climate change on lake temperatures. *Limnol. Oceanogr.* **62**, 2168–2178 (2017).
20. Gutowsky, L. F. G. et al. Quantifying multiple pressure interactions affecting populations of a recreationally and commercially important freshwater fish. *Glob. Chang. Biol.* **25**, 1049–1062 (2019).
21. Hansen, G. J. A., Read, J. S., Hansen, J. F. & Winslow, L. A. Projected shifts in fish species dominance in Wisconsin lakes under climate change. *Glob. Chang. Biol.* **23**, 1463–1476 (2017).
22. Honsey, A. E., Rypel, A. L. & Venturelli, P. A. Guidance for selecting base temperatures when using degree-days in fish growth analyses. *Can. J. Fish. Aquat. Sci.* **80**, 549–562 (2023).
23. Honsey, A. E., Feiner, Z. S. & Hansen, G. J. A. Drivers of walleye recruitment in Minnesota' s large lakes. *Can. J. Fish. Aquat. Sci.* **77**, 1921–1933 (2020).
24. Butcher, J. B., Nover, D., Johnson, T. E. & Clark, C. M. Sensitivity of lake thermal and mixing dynamics to climate change. *Clim. Chang.* **129**, 295–305 (2015).
25. Stefan, H. G., Fang, X. & Eaton, J. G. Simulated fish habitat changes in North American lakes in response to projected climate warming. *Trans. Am. Fish. Soc.* **130**, 459–477 (2001).
26. Fang, X., Stefan, H. G., Eaton, J. G., McCormick, J. H. & Alam, S. R. Simulation of thermal/dissolved oxygen habitat for fishes in lakes under different climate scenarios: Part 1. Cool-water fish in the contiguous US. *Ecol. Modell.* **172**, 13–37 (2004).
27. Gillis, D. P., Minns, C. K., Campana, S. E. & Shuter, B. J. Major changes in fish thermal habitat diversity in Canada's Arctic lakes due to climate change. *Commun. Earth Environ.* **5**, 89 (2024).
28. Missaghi, S., Hondzo, M. & Herb, W. Prediction of lake water temperature, dissolved oxygen, and fish habitat under changing climate. *Clim. Chang.* **141**, 747–757 (2017).
29. Hipsey, M. R. et al. A General Lake Model (GLM 3.0) for linking with high-frequency sensor data from the Global Lake Ecological Observatory Network (GLEON). *Geosci. Model Dev.* **12**, 473–523 (2019).
30. Hasnain, S. S., Shuter, B. J. & Minns, C. K. Phylogeny influences the relationships linking key ecological thermal metrics for North American freshwater fish species. *Can. J. Fish. Aquat. Sci.* **70**, 964–972 (2013).
31. Hasnain, S. S., Escobar, M. D. & Shuter, B. J. Estimating thermal response metrics for North American freshwater fish using Bayesian phylogenetic regression. *Can. J. Fish. Aquat. Sci.* **75**, 1878–1885 (2018).
32. Jobling, M. Temperature tolerance and the final preferendum—rapid methods for the assessment of optimum growth temperatures. *J. Fish. Biol.* **19**, 439–455 (1981).

33. Beitinger, T. L. & Fitzpatpick, L. C. Physiological and ecological correlates of preferred temperature in fish. *Am. Zool.* **19**, 319–329 (1979).
34. Cline, T. J., Bennington, V. & Kitchell, J. F. Climate change expands the spatial extent and duration of preferred thermal habitat for Lake Superior fishes. *PLoS ONE* **8**, e62279 (2013).
35. Corson-Dosch, H. R., Mcaliley, W. A., Platt, L. R. C., Padilla, J. A. & Read, J. S. Daily water column temperature predictions for thousands of Midwest U.S. lakes between 1979-2022 and under future climate scenarios. U.S. Geological Survey data release. https://doi.org/10.5066/P9EQQER7 (2023).
36. Coker, G. A., Portt, C. B. & Minns, C. K. Morphological and ecological characteristics of Canadian freshwater fishes. *Can. Manuscr. Rep. Fish. Aquat. Sci.* **2554**, 1–95 (2001).
37. Lyons, J. et al. Defining and characterizing coolwater streams and their fish assemblages in Michigan and Wisconsin, USA. *N. Am. J. Fish. Manag.* **29**, 1130–1151 (2009).
38. Maberly, S. C. et al. Global lake thermal regions shift under climate change. *Nat. Commun.* **11**, 1–9 (2020).
39. Woolway, R. I. & Merchant, C. J. Intralake heterogeneity of thermal responses to climate change: a study of large Northern Hemisphere Lakes. *J. Geophys. Res. Atmos.* **123**, 3087–3098 (2018).
40. Woolway, R. I. & Merchant, C. J. Worldwide alteration of lake mixing regimes in response to climate change. *Nat. Geosci.* **12**, 271–276 (2019).
41. Tong, Y. et al. Global lakes are warming slower than surface air temperature due to accelerated evaporation. *Nat. Water* **1**, 929–940 (2023).
42. Boehrer, B. & Schultze, M. Stratification of lakes. *Rev. Geophys.* **46**, 1–27 (2008).
43. Pilla, M. R. et al. Deeper waters are changing less consistently than surface waters in a global analysis of 102 lakes. *Sci. Rep.* **10**, 20514 (2020).
44. Woolway, R. I. The pace of shifting seasons in lakes. *Nat. Commun.* **14**, 1–10 (2023).
45. Pankhurst, N. W. & Munday, P. L. Effects of climate change on fish reproduction and early life history stages. *Mar. Freshw. Res.* **62**, 1015–1026 (2011).
46. Guzzo, M. M. & Blanchfield, P. J. Climate change alters the quantity and phenology of habitat for lake trout (*Salvelinus namaycush*) in small boreal shield lakes. *Can. J. Fish. Aquat. Sci.* **74**, 871–884 (2017).
47. Barta, M. E. et al. Lagging spawning and increasing phenological extremes jeopardize walleye (*Sander vitreus*) in north-temperate lakes. *Limnol. Oceanogr. Lett.* **9**, 229–236 (2024).
48. Farmer, T. M., Marschall, E. A., Dabrowski, K. & Ludsin, S. A. Short winters threaten temperate fish populations. *Nat. Commun.* **6**, 1–10 (2015).
49. Jobling, M. A. L. C. O. L. M. Temperature and growth: modulation of growth rate via temperature. *Glob. Warm. Implic. Freshw. Mar. fish. Soc. Exp. Biol. Semin. Ser.* **61**, 225–253 (1997).
50. Zhou, J. et al. Controls of thermal response of temperate lakes to atmospheric warming. *Nat. Commun.* **14**, 6503 (2023).
51. Jane, S. F. et al. Widespread deoxygenation of temperate lakes. *Nature* **594**, 66–70 (2021).
52. Smith, C. C. et al. Secondary forests offset less than 10% of deforestation-mediated carbon emissions in the Brazilian Amazon. *Glob. Chang. Biol.* **26**, 7006–7020 (2020).
53. Feiner, Z. S. et al. Resist-accept-direct (RAD) considerations for climate change adaptation in fisheries: the Wisconsin experience. *Fish. Manag. Ecol.* **29**, 346–363 (2022).
54. Jeppesen, E. et al. Impacts of climate warming on the long-term dynamics of key fish species in 24 European lakes. *Hydrobiologia* **694**, 1–39 (2012).
55. Daniel, W. M. & Neilson, M. E. Native ranges of freshwater fishes of North America (ver. 2.0, March 2022). U.S. Geological Survey data release. https://doi.org/10.5066/P9C4N10N (2022).

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L.X. conducted the analyses and wrote the manuscript. Z.S.F., P.F., G.J.A.H., R.L., C.P.P., M.V., L.W., and O.P.J. provided comments and contributed substantive revisions to the manuscript.

Competing interests
The authors declare no competing interests.

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