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Climate change vulnerability of Arctic char across Scandinavia

Clint C. Muhlfeld[1] | Timothy J. Cline[2] | Anders G. Finstad[3,4] | Dag O. Hessen[5] | Sam Perrin[4] | Jens Thaulow[6] | Diane Whited[7] | Leif Asbjørn Vøllestad[5]

[1]U.S. Geological Survey, Northern Rocky Mountain Science Center, West Glacier, Montana, USA

[2]Department of Ecology, Montana State University, Bozeman, Montana, USA

[3]Department of Natural History, NTNU University Museum, Norwegian University of Science and Technology, Trondheim, Norway

[4]Gjærevoll Center for Biodiversity Foresight Analyses, Norwegian University of Science and Technology, Trondheim, Norway

[5]Department of Biosciences, University of Oslo, Oslo, Norway

[6]Formerly Employed at Norwegian Institute for Water Research, Oslo, Norway

[7]Flathead Lake Biological Station, University of Montana, Polson, Montana, USA

Correspondence

Clint C. Muhlfeld, U.S. Geological Survey, Northern Rocky Mountain Science Center, Glacier National Park, 38 Mather Drive, West Glacier, MT 59936 USA.

Email: cmuhlfeld@usgs.gov

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Abstract

Climate change is anticipated to cause species to shift their ranges upward and poleward, yet space for tracking suitable habitat conditions may be limited for range-restricted species at the highest elevations and latitudes of the globe. Consequently, range-restricted species inhabiting Arctic freshwater ecosystems, where global warming is most pronounced, face the challenge of coping with changing abiotic and biotic conditions or risk extinction. Here, we use an extensive fish community and environmental dataset for 1762 lakes sampled across Scandinavia (mid-1990s) to evaluate the climate vulnerability of Arctic char (*Salvelinus alpinus*), the world's most cold-adapted and northernly distributed freshwater fish. Machine learning models show that abiotic and biotic factors strongly predict the occurrence of Arctic char across the region with an overall accuracy of 89 percent. Arctic char is less likely to occur in lakes with warm summer temperatures, high dissolved organic carbon levels (i.e., browning), and presence of northern pike (*Esox lucius*). Importantly, climate warming impacts are moderated by habitat (i.e., lake area) and amplified by the presence of competitors and/or predators (i.e., northern pike). Climate warming projections under the RCP8.5 emission scenario indicate that 81% of extant populations are at high risk of extirpation by 2080. Highly vulnerable populations occur across their range, particularly near the southern range limit and at lower elevations, with potential refugia found in some mountainous and coastal regions. Our findings highlight that range shifts may give way to range contractions for this cold-water specialist, indicating the need for pro-active conservation and mitigation efforts to avoid the loss of Arctic freshwater biodiversity.

KEYWORDS

Arctic char, Arctic freshwater ecosystems, climate vulnerability, extinction risk, range contractions, Scandinavia

1 | INTRODUCTION

Arctic freshwater ecosystems are experiencing profound environmental changes due to climate change and multiple anthropogenic stressors (Heino et al., 2009; Li et al., 2022; Sala et al., 2000; Su et al., 2021). The Arctic region is warming four times faster than the global average, altering water temperature, hydrological regimes, water quality, and food webs within freshwater ecosystems (Feng et al., 2021; Saros et al., 2023; Wrona et al., 2016). As temperatures increase and exceed thermal limits, many cold-water species are experiencing declines in distribution and abundance, while cool- and warm-water species are expanding into higher elevations and latitudes, potentially displacing cold-adapted species (Barbarossa et al., 2021; Reist, Wrona, Prowse, Power, Dempson, King, et al., 2006). Human activities, such as land-use changes, pollution, and introduction and spread of invasive species, are further accelerating freshwater biodiversity loss (Perrin et al., 2021; Reid et al., 2019). Climate change and landscape alterations are increasing precipitation and forest cover (Heino et al., 2009), leading to permafrost thaw (Vonk et al., 2015) and elevated dissolved organic carbon runoff, resulting in the "browning" (Crapart et al., 2023; de Wit et al., 2016; Finstad et al., 2016; Larsen et al., 2011) and disruption of freshwater ecosystems (Finstad et al., 2014; Hayden et al., 2019; Karlsson et al., 2009). These combined stressors are posing significant threats to Arctic freshwater species and biodiversity, warranting broad-scale research to understand and mitigate their ecological impact, particularly on climate-sensitive, cold-water species.

Salmonid fishes are especially sensitive to climate change and altered environmental conditions because they require cold-water habitats that are increasingly fragmented by human activities, thereby forcing populations to tolerate environmental conditions in situ (Kovach et al., 2016). Consequently, many native trout and char species and lineages are endangered across the Northern Hemisphere (Muhlfeld et al., 2018; Muhlfeld et al., 2019). Arctic char (*Salvelinus alpinus*) is the most cold-adapted and northerly distributed freshwater fish globally that may be especially sensitive to climate change (Layton et al., 2021; Reist, Wrona, Prowse, Power, Dempson, Beamish, et al., 2006). It is also a socioeconomically important species for both recreational fishing and consumption (Klemetsen, 2013). However, populations have significantly declined, particularly in the southern part of their Holarctic range, with peripheral populations persisting in cold, deep lakes at temperate latitudes (Kelly et al., 2020). The decline of Arctic char has been attributed to various human-driven impacts, including climate change, habitat loss, overfishing, pollution, invasive species, and complex interactions among these stressors (Weinstein et al., 2024). Global climate change is anticipated to further endanger Arctic char by warming habitats beyond their thermal preference (i.e., 0–10°C) (Hein et al., 2012; Larsson, 2005). As a result, Arctic char populations may face increased vulnerability to decline or extirpation in the face of ongoing climate change and other anthropogenic pressures. Thus, uncovering complex relationships between environmental conditions and Arctic char distribution is particularly important for understanding how future climate change may affect the persistence of this cold-adapted species and biodiversity of Arctic freshwater ecosystems.

Climate change vulnerability assessments are valuable tools for identifying species that are most likely to be vulnerable to the impacts of climate change (Foden et al., 2018; Pacifici et al., 2015). By evaluating the sensitivity and exposure of species to various climatic and environmental changes, vulnerability assessments can help assess species' risks of extinction or decline, identify geographic areas or populations of concern, and guide conservation efforts to mitigate climate change impacts. However, in recent decades there has been a growing interest in assessing the climate vulnerability of freshwater species based on downscaled models of temperature that predict habitats where temperatures will be within the thermal limits of cold-water fishes (Kovach et al., 2016). Yet, such approaches fail to consider complex interactions between multiple environmental stressors and their combined effects on the persistence of species under future climatic conditions (Pacifici et al., 2015). Machine learning techniques (e.g., random forest, neural networks, etc.) are increasingly used in ecological research for identifying the environmental factors that influence species distribution across diverse landscapes (Lucas, 2020). Machine learning algorithms, trained on large and complex datasets, capture non-linear relationships between species occurrence and environmental variables, improving prediction accuracy and potentially revealing complex ecological interactions among variables (Breiman, 2001). As such, these approaches may provide powerful insights into species' vulnerability to climate change and for guiding effective climate adaptation and conservation strategies (Cutler et al., 2007).

Studies examining how climate change and environmental conditions influence the vulnerability of cold-adapted species across high-latitude landscapes are needed for predicting the future of Arctic freshwater biodiversity. Here, we quantify the vulnerability of Arctic char to future climate change across Scandinavia. Using an extensive dataset of fish species occurrence and environmental information from 1762 lakes sampled in the mid-1990s (herein referred to as "baseline" conditions), we use a random forest model to predict Arctic char distribution under future climate scenarios (mid and late 21st century). Results provide a comprehensive assessment of the environmental factors influencing the distribution of Arctic char across diverse Arctic landscapes and identify potential refugia for persistence of this cold-adapted species under future climate warming.

2 | MATERIALS AND METHODS

2.1 | Fish community and environmental data

We combined extensive datasets on fish communities, climate, and limnological parameters to assess the environmental factors influencing the distribution of Arctic char in 1762 Scandinavian lakes (Norway, Sweden, and Finland) sampled in the mid-1990s. Lakes were selected from the 1995 Northern European Lake Survey, which aimed to evaluate water quality (Henriksen et al., 1998). Fish community data were obtained by co-authors in Scandinavia from the 1995–1997 Nordic Lakes Fish Survey, which aimed to assess the status of fish populations in Fennoscandian lakes (≥0.04 km^2) (Tammi et al., 2003). Fish presence–absence data were obtained using standardized questionnaires (Hesthagen et al., 1993; Hesthagen et al., 1999; Tammi et al., 2003), targeting local experts like landowners and municipal environmental managers. Method validity was confirmed by cross-referencing with test-fishing data, which have proven highly reliable for Norwegian lakes with limited fish species (Hesthagen et al., 1993). In addition, we restricted the geographical area to the known historical distribution of Arctic char to avoid false absences, using either maps georeferenced from literature sources (Daverdin et al., 2019; Huitfeldt-Kaas, 1918) or, since Arctic char is an anadromous fish originally immigrating to Scandinavia from the sea after the last ice-age, the historical high sea level delineation. Historical sea levels were compiled from the Finland Geological Survey, Geological Survey of Sweden, and Norway. Predictor variables for modeling the distribution of Arctic char (see Section 2.2 below) included water chemistry attributes (total phosphorus (P), total organic carbon (TOC), and pH; Henriksen et al., 1998), biotic interactions (occurrence of brown trout and northern pike; Tammi et al., 2003), human disturbance (i.e., Human Footprint estimated in 1993) (Venter et al., 2016), and lake area (Henriksen et al., 1998). Additionally, we used end of the 20th century climate simulations (1961–1990) of mean summer air temperature and mean summer precipitation to characterize baseline climatic conditions for each lake, which allowed us to consistently project potential changes in Arctic char distribution under future climate warming scenarios (see Section 2.3 below) (Navarro-Racines et al., 2020).

2.2 | Occurrence modeling

We used random forest models (Cutler et al., 2007) to quantify the importance and estimate the partial dependence of several abiotic and biotic factors on the presence and absence of Arctic char in lakes (Figure S1). To increase the predictive accuracy of the analysis, random forest models were trained on half of the dataset and fitted to the other half of the data. In our dataset, absences are much more common (1433 absences and 329 presences); therefore, we used a stratified random forest where each tree was fit to a random sample of 150 presences and 150 absences. We assessed a range of stratified sample sizes, and the choice of stratification sample size did not change the accuracy of the model or covariate effects. We fit random forest models including 5000 trees using the "randomForest" package in R (R Core Team, 2023).

To assess the strength of covariate effects on Arctic char occurrence, we calculated variable importance using the mean decrease in the Gini impurity metric. This metric measures the model's ability to correctly classify presence or absence for each covariate (node purity) and is valuable for use in classification analyses (Cutler et al., 2007). A larger number indicates that when a variable is included in a tree the rate of correct classification is increased. Other measures of variable importance (e.g., mean accuracy decrease) yielded similar results, except for the presence of brown trout being an important predictor of Arctic char presence (see Section 4). To assess the direction and overall shape of each covariate effect and interactions between variables on Arctic char presence, we calculated the partial dependence using the "pdp" package in R. While variables in a random forest model do not need to be transformed to meet parametric assumptions, we log-transformed total organic carbon, precipitation, total phosphorus, lake area, and human footprint because of their skewed distributions to make the interpretation of partial effects easier.

2.3 | Future predictions

We used climate projections from CMIP5 to assess the potential impact of future climate change on Arctic char lake habitats (Navarro-Racines et al., 2020). An ensemble of three General Circulation Models (GCMs) (GFDL-ESM2M, BCC-CSM1, and MPI-ESM-LR) was employed to optimize the simulation of mean summer air temperatures (July through September) across Scandinavia (1 km^2 resolution). This simulation covered historical conditions (1961–1990) and future climate scenarios for the 2050s (2040–2069) and 2080s (2070–2099) under representative concentration pathways (RCPs) 4.5 and 8.5. RCP 4.5 represents a future with moderate greenhouse gas emissions, resulting in a radiative forcing increase of 4.5 watts per square meter by 2100. Conversely, RCP 8.5 depicts a high-emission future where greenhouse gas concentrations continue to rise unabated, leading to a radiative forcing of 8.5 watts per square meter by the year 2100.

To predict the future occurrence of Arctic char under different climate scenarios, we used the fitted random forest model with predictions of future temperatures under two future climate scenarios and two different time periods: RCP 4.5 (2050 and 2080) and RCP 8.5 (2050 and 2080). Thresholds of a modeled probability of Arctic char occurrence from the fitted random forest model were used to determine risk categories for future predictions of Arctic char presence under various climate scenarios (Figure S2). The vast majority of observed Arctic char presences (87%) occurred where the modeled probability of occurrence was greater than .8, and no presences were observed in lakes with a modeled probability less than .6. Therefore, we used these values to set vulnerability thresholds for future presence. Lakes where the probability of occurrence in a future scenario was greater than .8 were considered low risk, lakes where the future probability of occurrence was less than .6 were considered high risk, and lakes between .6 and .8 were considered moderate risk. All other variables were assumed to be unchanged in future scenarios, yet their effects moderate risk through interactions within the model.

3 | RESULTS

Environmental conditions strongly influenced the spatial distribution of Arctic char across Scandinavian lakes (Figure 1; Figure S1). The full random forest model correctly classified the presence or absence of Arctic char in 89% of sampled lakes (Table S1). The probability of Arctic char presence decreased with increased summer temperatures, TOC concentrations, and the presence of northern pike (Figure 2a). Among these factors, temperature had the strongest effect on the distribution of Arctic char, as they rarely were predicted to occur in lakes with mean summer air temperatures above 13°C (Figure 2b). Moreover, Arctic char were notably absent from lakes with TOC concentrations exceeding 4.5 mg/L, indicating a strong negative effect of water browning on their occurrence (Figure 2c). The presence of northern pike showed a significant biotic interaction with Arctic char, reducing their likelihood of occurrence by approximately half in lakes where northern pike were present (Figure 2d).

There were also important interactive effects among some of the abiotic and biotic variables influencing Arctic char occurrence. Specifically, lake area moderated the negative effects of warm temperatures and interactions with northern pike (Figure 3a,b). In lakes where air temperatures exceeded 13°C, Arctic char were 1.5 times more likely to occur in larger lakes with an area greater than 3 km^2, likely due to the increased availability of deep cold-water refuges (Figure 3a). Additionally, larger lakes (Figure 3b) and those with colder temperatures (Figure 3c) demonstrated a higher probability of Arctic char coexistence with northern pike. These findings highlight the importance of lake size (and volume) in moderating the impacts of temperature and biotic interactions on Arctic char distribution.

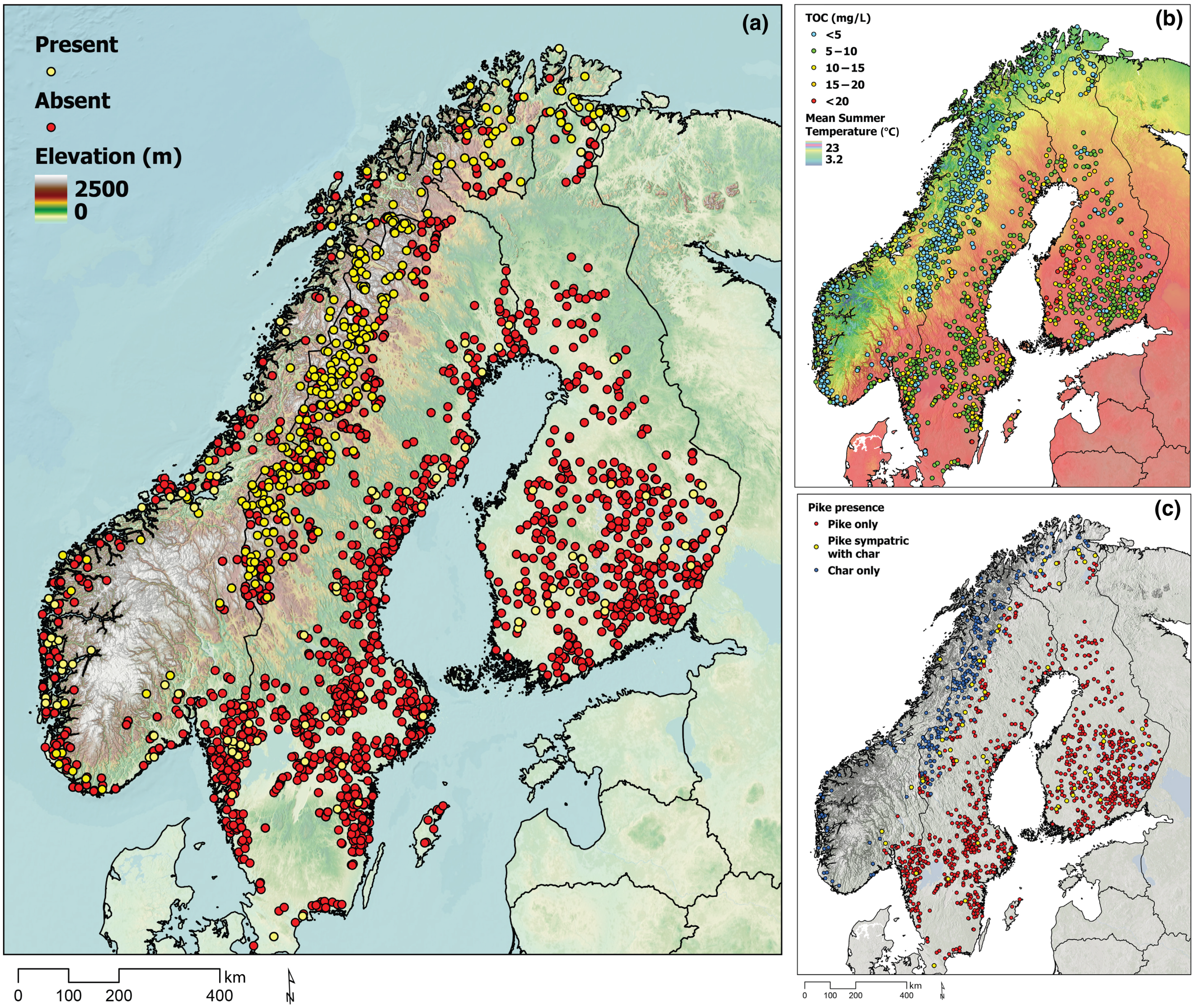

FIGURE 1 Spatial distribution of Arctic char across Scandinavia. (a–c) Maps showing the sampling locations and occurrence of Arctic char (Tammi et al., 2003) in relation to elevation (a), total dissolved carbon (TOC) (Henriksen et al., 1998) and mean summer temperature (b) (Navarro-Racines et al., 2020), and northern pike occurrence (c) (Tammi et al., 2003). Summary data are included in Figure S1. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

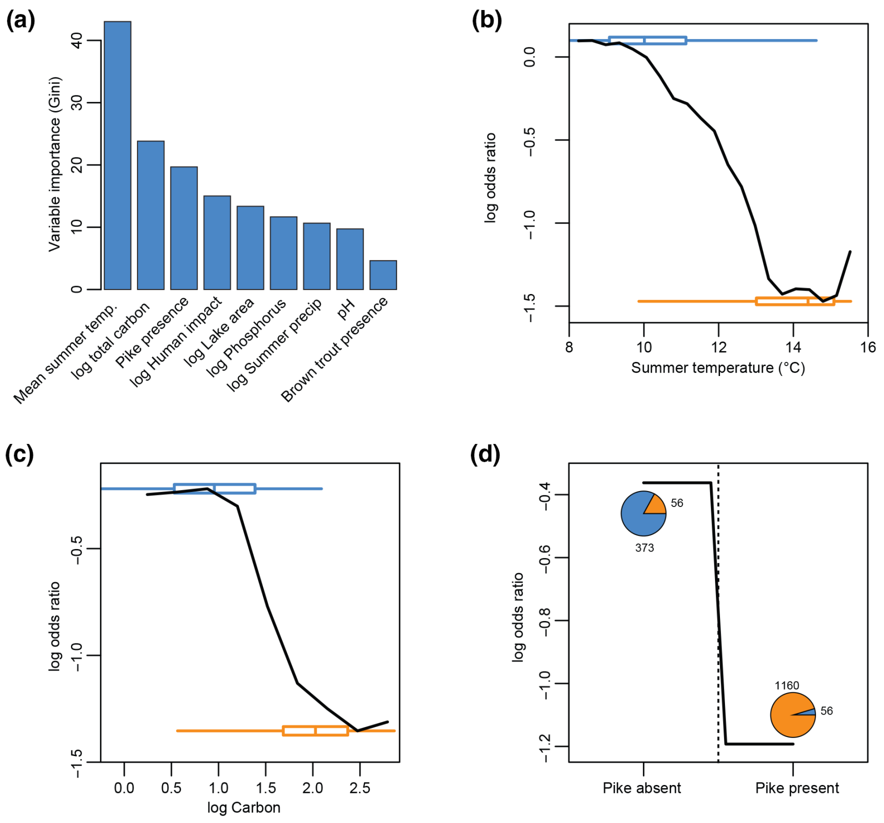

FIGURE 2 Environmental factors influencing the distribution of Arctic char. (a) Variable importance for random forest regression of Arctic char occurrence against environmental variables. Variables are ordered from highest to lowest by random forest variable importance (see Section 2). The full random forest regression model is 88.5% accurate in predicting the presence or absence of Arctic char (a). Partial dependence plots of temperature (b), total organic carbon (natural log) (c), and northern pike (presence/absence) (d) on the occurrence of Arctic char. Box plots along the x-axes denote the range of observed presences (blue) and absences (orange) for a given predictor. Pie charts in panel b show the proportion of Arctic char presences relative to northern pike presences (orange) and absences (blue).

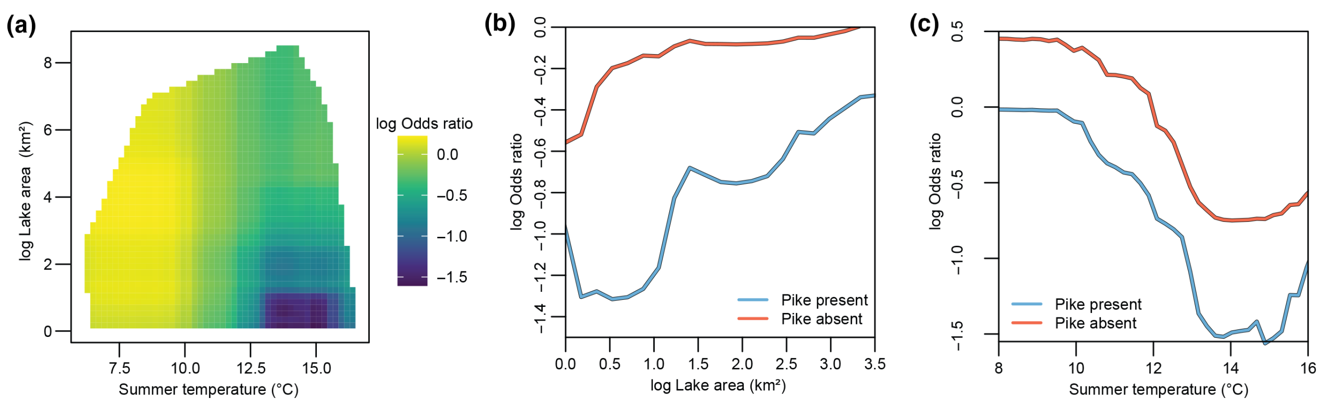

FIGURE 3 Interactive effects of abiotic and biotic factors influencing the occurrence of Arctic char. (a–c) Partial dependence of the interactive effects between lake area and summer temperature (a), lake area and northern pike occurrence (b), and summer temperature and northern pike occurrence (c) on the occurrence of Arctic char.

Future climate change is predicted to significantly reduce the extent of suitable lake habitats supporting Arctic char. We modeled future habitat conditions and the occurrence of Arctic char under future temperature warming (RCP4.5 and RCP8.5) scenarios. Our projections suggest a 40%–80% decline in suitable habitats that are likely to support populations persisting on the landscape by the end of the 21st century. Warming projections under the RCP4.5 emission scenario suggest that 29% of extant populations (baseline) are at high risk of extirpation by 2050 (Figure 4a) and 42% by 2080 (Figure 4b), while 45% have a medium risk of extirpation by 2050 (Figure 4a) and 44% by 2080 (Figure 4b). Under the RCP8.5 scenario, warming projections indicate a more pronounced trend: by 2050, 52% of populations face a high risk of extirpation (Figure 4c), rising to 81% by 2080 (Figure 4d), while 40% face medium risk by 2050 (Figure 4c), declining to 16% by 2080 (Figure 4d). These results suggest significant range contractions in Scandinavian lakes for this cold-adapted species, primarily in warm, lower-elevation lakes with high TOC concentrations, predominantly at the southern range limit. Under the RCP4.5 scenario, populations with a low risk of extirpation are projected to decrease from 26% by 2050 (Figure 4a) to 14% by 2080 (Figure 4b), while under the more severe RCP8.5 scenario, those numbers drop from 8% by 2050 (Figure 4c) to a mere 2% by 2080 (Figure 4d). These low-risk populations are likely to persist

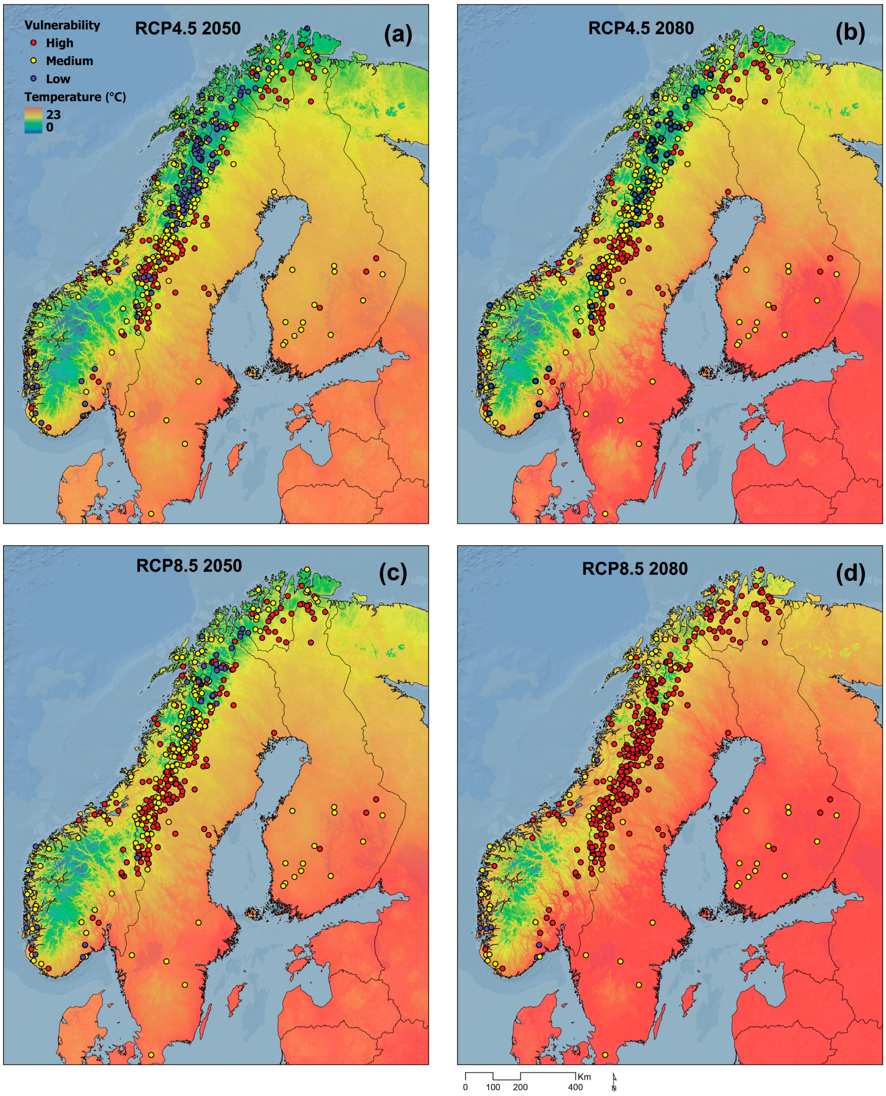

FIGURE 4 Projected extirpation risk of Arctic char under future climates. Projected extirpation risk (vulnerability) for Arctic char populations under future climate warming scenarios: RCP4.5 2050 (a) and 2080 (b) and RCP8.5 2050 (c) and 2080 (d). Extirpation risk is calculated from the future probability of occupancy (*p*) for Arctic char under each scenario. Red dots indicate high risk ($p < .6$), yellow medium risk ($p = .6–.8$), and blue are low risk ($p > .8$). Map lines delineate study areas and do not necessarily depict accepted national boundaries.

at higher latitudes and elevations in the mountainous regions and along the coastal areas of the Norwegian Sea.

4 | DISCUSSION

Species distribution models have been widely applied as decision-support tools for strategic adaptation and conservation planning for freshwater species. However, most approaches are based on downscaled models of water temperature that predict habitats where temperatures will be within the thermal limits of cold-water fishes (Armstrong et al., 2021). Such climate-envelope approaches often neglect how changes in temperature interact with other environmental factors to affect species' distribution (Foden et al., 2018). We used an extensive environmental monitoring dataset and advanced machine learning to evaluate the complex interplay of environmental, physical, and physiological factors influencing the occurrence of Arctic char. Random forest models demonstrate that abiotic and biotic factors strongly influence Arctic char occurrence, with lakes experiencing warm summer temperatures, high TOC levels, and northern pike being less likely to support Arctic char under baseline (1990s) and future warming (2050 and 2080) conditions. These findings underscore the importance of considering these complexities in climate vulnerability assessments and conservation planning for freshwater species.

Water browning has a strong negative effect on Arctic char presence in Scandinavian lakes. Water browning can disrupt lake food webs by decreasing water transparency, benthic primary production, and thus dissolved oxygen concentrations (Thrane et al., 2014; Vasconcelos et al., 2019). Water browning likely affects the foraging ability (i.e., search field) and food resources available to Arctic char (Karlsson et al., 2009), with the potential to ultimately affect population production (Finstad et al., 2014; Karlsson et al., 2009). Browning also affects thermal stratification (i.e., more heat trapped in the upper part of the water column), causing increased resistance toward mixing (Palmer et al., 2014). In addition, increased inputs of organic C not only reduce photosynthesis with depth, but also increase microbial respiration. The sum of these effects is likely to reduce deep-water oxygen concentrations, posing a specific challenge to an oxygen-demanding lake spawner like Arctic char.

Understanding how ecosystems respond to climate change depends on examining how habitat conditions interact with the prevailing climate (Parmesan, 2006). Our study revealed that larger lakes can mitigate the adverse impacts of warm temperatures and interactions with northern pike on Arctic char presence. We found that larger lakes (>3 km^2) are 1.5 times more likely to host Arctic char in areas with average air temperatures exceeding 13°C. These larger lakes also facilitate the coexistence of Arctic char with northern pike, which typically affect char occurrence. Northern pike tend to outcompete and prey on Arctic char in warmer, more productive lakes, while Arctic char tend to thrive in smaller, colder, oligotrophic lakes with extended ice cover (Hein et al., 2012). These deep, large lakes create colder, oxygen-rich layers through thermal stratification, providing a stable thermal environment for cold-adapted fishes like Arctic char. As global temperatures rise, these deep, cold lakes will serve as critical refuges for Arctic char, enabling them to coexist with competitors and predators like northern pike.

The presence of brown trout did not strongly influence the occurrence of Arctic char, likely due to their coexistence in larger lakes and shared preference for cold temperatures. While brown trout presence was a good predictor of Arctic char presence, it performed poorly in discriminating between presences and absences. These results suggest that at a broad scale, the geographic distribution of these species is similar, making brown trout presence a good indicator of suitable habitat for Arctic char. At smaller scales, the geographical distributions of these cold-water species are primarily influenced by ecosystem productivity and competitive interactions, with Arctic char favoring cold, low-productivity lakes and brown trout favoring warmer, more productive lakes (Finstad et al., 2011). In sympatric conditions, interspecific competition can lead to the displacement of Arctic char from littoral habitats (Elliott & Elliott, 2010; Eloranta et al., 2013), while warming temperatures and decreased oxygen levels may further limit suitable Arctic char habitats (Elliott & Elliott, 2010). Climate change and anthropogenic stressors may disproportionately reduce lake habitat niches available for Arctic char, potentially allowing brown trout to expand into vacant niches (Hein et al., 2012). This expansion may negatively impact Arctic char abundance, a dynamic not fully captured in our presence-only analysis.

Our results portend significant range contractions of Arctic char across Scandinavia due to future global warming, particularly near the southern range limit and at lower elevations. Under a conservative emission scenario (RCP4.5), 42% of populations face high risk of extirpation by the end of the 21st century, increasing to 81% under a high-emission scenario (RCP8.5). These results substantiate other studies projecting significant climate-induced range contractions at smaller geographical scales. For example, Hein et al. (2012) predicted a 73% range reduction in Swedish lakes by 2100. Range contractions are expected primarily in warm, lower elevation lakes with high TOC concentrations, mostly at the southern range limit. Projections indicate that only 14% and 2% of populations are estimated to face low risk of extirpation by 2080 under RCP4.5 and 8.5 scenarios, respectively. Low-risk populations are likely to persist at higher latitudes and elevations in the mountainous regions and coastal areas of the Norwegian Sea. Notably, our "baseline" datasets originate from the 1990s, and current fish distribution and environmental conditions may have changed since then. These results can inform management strategies to restore and protect critical habitats, and to identify and prioritize "climate refugia" that support species persistence as the climate continues to warm and transform the Arctic's freshwater ecosystems.

The persistence of many species is ultimately linked to whether they can adapt in place to rapid environmental changes or shift their distribution to track suitable habitats. For range-restricted freshwater species like Arctic char, the greatest challenges of climate adaptation will be related to adaptive capacity, dispersal ability, and habitat alterations. While Arctic char have demonstrated phenotypic adaptability to rapidly changing temperatures (Hooker et al., 2023), their potential for northward and upward expansion is limited unless new habitats emerge from retreating glaciers (Pitman et al., 2020), especially in polar regions such as Svalbard. Consequently, shifts in habitat conditions and connectivity are anticipated to reduce overall distribution and abundance, increase isolation, diminish gene flow, and erode genetic and ecological diversity–critical for adaptation and resiliency. Additionally, Arctic char display considerable intra-species diversity, with individuals within lakes varying in morphology, behavior, and life history (Klemetsen et al., 2003; Weinstein et al., 2024). This diversity may stem from differences in genetic populations or phenotypic plasticity, related to feeding niches, spawning locations, and phenology (Brunner et al., 2001; Klemetsen, 2010). While our study assumes uniform responses to environmental stressors within each lake, it is important to acknowledge that the loss of genetically distinct populations may exceed our predictions, thus magnifying the predicted loss of diversity.

These findings enhance our understanding of the abiotic and biotic factors influencing Arctic char populations and their vulnerability to climate change across Arctic landscapes. The interaction between climatic and anthropogenic stressors underscores the urgency of developing proactive climate adaptation and mitigation strategies to protect populations and diverse habitats in high-latitude landscapes. Conservation strategies might include protecting climate refugia, restoring habitat diversity and connectivity, translocating imperiled populations, establishing native fish reserves, and minimizing anthropogenic impacts such as pollution, habitat destruction, and exotic species introductions. Such conservation measures may hold promise for enhancing the adaptation and resilience of Arctic char and other cold-water species to impending climate warming across high-latitude landscapes.

AUTHOR CONTRIBUTIONS

Clint C. Muhlfeld: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; writing – original draft; writing – review and editing. **Timothy J. Cline:** Formal analysis; methodology; writing – original draft; writing – review and editing. **Anders G. Finstad:** Data curation; methodology; writing – review and editing. **Dag O. Hessen:**

Conceptualization; data curation; formal analysis; funding acquisition; investigation; project administration; resources; writing – original draft; writing – review and editing. **Sam Perrin:** Data curation. **Jens Thaulow:** Data curation; writing – review and editing. **Diane Whited:** Data curation; formal analysis; methodology; writing – review and editing. **Leif Asbjørn Vøllestad:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; project administration; resources; writing – original draft; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest present.

DATA AVAILABILITY STATEMENT

The data and code that support the findings of this study are openly available in Zenodo at https://doi.org/10.5281/zenodo.11459009. Lake location and fish occurrence was accessed from the Norwegian Institute for Nature Research and are available upon request. Lake area and biogeochemistry was accessed from the Norwegian Institute for Water Research Repository at https://niva.brage.unit.no/niva-xmlui/handle/11250/209342. Human Footprint maps were accessed from https://datadryad.org/stash/dataset/doi:10.5061/dryad.052q5. Climate data were accessed from http://ccafs-climate.org/.

ORCID

Clint C. Muhlfeld https://orcid.org/0000-0002-4599-4059
Timothy J. Cline https://orcid.org/0000-0002-4955-654X
Anders G. Finstad https://orcid.org/0000-0003-4529-6266
Dag O. Hessen https://orcid.org/0000-0002-0154-7847
Sam Perrin https://orcid.org/0000-0002-1266-1573
Jens Thaulow https://orcid.org/0000-0002-4063-6738
Diane Whited https://orcid.org/0000-0002-6255-715X
Leif Asbjørn Vøllestad https://orcid.org/0000-0002-9389-7982

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