Velocity of climate change and the vulnerability of mountain lake landscapes

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Abstract

Freshwater ecosystems in mountain landscapes are increasingly threatened by climate change. Accumulated heat in ecosystems can result in lethal short-term heat exposure, while the velocity of change governs severity and rates of long-term heat exposure. Here, we novelly integrate heat accumulation and velocity of change approaches to classify climate-vulnerable USA mountain lake watersheds. Our results broadly demonstrate how rates of heat accumulation are increasing across mountain landscapes, and that this rise is most pronounced at lower elevations. We estimate 19% of mountain watersheds are currently at greatest vulnerability, and this value is set to jump to 33% by end-of-century. Further, mean killing degree days (i.e., mean number of days above 90th percentile) will increase 215 – 254% (mean = 236%) over this same timeframe. Taken together, results indicate heat accumulation will increase substantially over the next 75 years; changes will be experienced most severely in lower elevation landscapes and those with the greatest historical velocity of change. This degree of climate change will likely restructure species' distributions. Decision-makers can utilize these classifications to understand landscapes likely to support desired species and ecosystem services into the future, thereby enabling more effective allocation of limited conservation resources.

Significance Statement

The velocity at which mountain lake landscapes are undergoing thermal change is poorly understood. Our results show how, and which, mountain landscapes are vulnerable to unprecedented heat accumulation.

Author Contributions:

Conceptualization: **CAP, ALR**

Code, Data Investigation, & Formal Analysis: **CAP**

Data Visualization: **CAP, ALR**

Data Interpretation: **CAP, JAW, SS, ALR**

Writing – original draft: **CAP**

Writing – review & editing: **CAP, JAW, SS, ALR**

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Introduction

Rates of freshwater biodiversity loss outpace those of other environments, and protections for freshwater ecosystems are insufficient at almost all scales (Reid et al. 2019; Tickner et al. 2020; Flitcroft et al. 2023). Freshwater ecosystems are in global peril; human domination of the global water cycle undermines ecosystem stability and disrupts ecological organization (Baron et al. 2002; Woodward et al. 2010; Collen et al. 2014). Climate change is desiccating wetlands, accelerating glacial retreat, and producing cascading consequences to ecosystem regimes, food web structure, and community functions (Carpenter et al. 1992; Ledger et al. 2013; Xu et al. 2019). Indeed, impacts of climate change are triggering disruptions across all levels of organization in freshwater ecosystems (Carpenter et al. 1992; Woodward et al. 2010; Knouft and Ficklin 2017). Climate-driven environmental disruption may be especially disruptive in mountain ecosystems, where terrestrial and freshwater taxa interact and often subsidize one another (Nakano et al. 1999; Piovia-Scott et al. 2016; Rolla et al. 2018). Mountain species possess narrow thermal tolerances and restricted range distribution, thus climate adaptation via dispersal is highly limited (Sunday et al. 2019; Viterbi et al. 2020).

Temperature, particularly water temperature, is perhaps the most important ecological variable mediating key ecological processes in aquatic ectothermic species (Magnuson et al. 1979). Understanding the role of temperature in regulating the distribution of organisms is therefore widely recognized as critical for understanding and managing freshwater biodiversity (Lyons et al. 2009; Rypel 2014b; Lusardi et al. 2021). Mountain lake landscapes are already thought to be exceptionally vulnerable to climate change (Ficke et al. 2007; Bonacina et al. 2023; Prather et al. 2023). Therefore, quantifying heat accumulation and heat content of these areas is important (Vanderkelen et al. 2020). Nevertheless, nuance in how thermal regimes (i.e., the timing, magnitude, and velocity of temperature change or heat accumulation) holistically respond to climate change is important to quantify and understand (Willis et al. 2021). Short-term buildup of heat in aquatic ecosystems can lead to brief but lethal heat exposures, yet the velocity of this thermal change governs severity and long-term rate of exposure on the landscape. Velocity of change in particular is a useful lens through which to understand not only the magnitude of climate change experienced by organisms, but also the quickening pace of that change (Scheffer 1990; Barnett et al. 2015; Rypel In Revision.). For example, high velocity of change in ecosystems is associated with ecosystem fragility and abrupt shifts to alternate stable states (Scheffer and Carpenter 2003; Carpenter et al. 2017; Collins et al. 2018).

The consequences of potential increased velocity of climate change not only impacts aquatic ecosystems within catchments, but also the entire surrounding landscape (Greig et al. 2012; Larsen et al. 2016). Kratz et al. 1997 described the position of a lake within landscapes as a combination of the spatial and ecohydrological contexts of a lake within larger lake districts. Climate-driven niche ranges of many mountain organisms are shifting upslope toward more suitable habitat, such as those of alpine grouse and hares (Schai-Braun et al. 2021), plants (Inouye 2020; Richman et al. 2020), forest species and forest type (Abbasi et al. 2024), macroinvertebrates (Shah et al. 2012; Suzuki et al. 2024), ungulates (Büntgen et al. 2017), songbirds (Van Tatenhove et al. 2019), and a wide variety of other animals and fungi (Mamantov et al. 2021; Vitasse et al. 2021). Species range shifts in turn spur novel species interactions within native and expanded ranges (Alexander et al. 2015; Shepard et al. 2021; Abbasi et al. 2024) and has the potential to alter or displace species' functional roles within their ecosystems (Bender et al. 2019; Richman et al. 2020; Balik et al. 2023). For lakes specifically, warming temperatures influence community composition and biomass for diverse taxa (Jeppesen et al.

2010; Yvon-Durocher et al. 2011; Kuefner et al. 2021). Additionally, changing lake stratification dynamics, and warming water temperatures coupled with increasing prevalence of lake browning is reducing availability of coldwater fish habitat (Jane et al. 2024).

Novel conservation prioritization frameworks will assist practitioners in taking well-informed management action towards adapting to and mitigating increased velocity of change. More specifically, understanding how divergent ecosystems across mountain landscapes will respond to rising rates of heat accumulation anticipated by the end of the century will be important for deciphering which lake landscapes are most vulnerable to shifts (Adrian et al. 2009). Managers, especially those tasked with conservation prioritization of sensitive aquatic systems, their flora, and their fauna, have relatively few tools or science-based strategies to triage their resources effectively (Tulloch et al. 2015). Therefore, a vulnerability classification of lake landscape regions based on heat accumulation and velocity of change would be of wide appeal within the environmental management community.

In this study, we characterize climate vulnerability for all major USA mountain lake landscapes based on degree to which they have accumulated heat, historically and to end-of-century, as well as their experienced rate of change. Our specific goals were to: (1) Quantify heat, and harmful heat, accumulation across USA mountain lake landscapes over time. (2) Quantify experienced velocity of thermal change across these same lake landscapes. (3) Provide a mountain lake landscape classification based on heat accumulation such that any mountain lake landscape can be classified into one of three vulnerability types. (4) Quantitatively evaluate how lake landscape vulnerability, and lake classification, change over time under the modest SSP 3 / RCP 7.0 climate scenario.

Methods

Datasets

Spatialized lake polygon data for the United States (USA) were acquired from the National Hydrography Database (NHD) with the {nhdR} package (version 0.6.1) (Stachelek 2019; USGS 2022). The NHD contains comprehensive and standardized spatial distributions of surface waters (e.g., lakes, ponds, streams, rivers, canals) throughout the USA. Only waterbodies with the "Lake/Pond" designation in the NHD were used in this analysis (0-497 km^2 in surface area). The NHD was best suited for this study because it best captured mountain lakes, which are often small and miscounted, when compared to other popular databases.

Spatial NHD lake data (representing locations of "*Watersheds*" in the lake landscape, later joined to air temperature data) were joined to the Omernik Level III ecoregions framework (*https://www.epa.gov/eco-research/ecoregions*) (Omernik 1995; Omernik and Griffith 2014) and cropped to contain lake-watershed points within mountainous polygons for each of the 10 primary mountain ranges in the contiguous United States, contemporarily named: Appalachian/Atlantic Maritime Highland (n = 10,467), Arizona–New Mexico (n = 1,033), Blue (n = 284), Blue Ridge (n = 464), Cascade (n = 2,165), Idaho Batholith (n = 1,035), Klamath (n = 245), Rocky/Colombia (n = 9,661), Sierra Nevada (n = 2,358), Wasatch–Uinta (n = 988). We note that these coordinates are meant to merely represent key locations on the landscape (i.e., "*Watersheds*" of the lake landscape) despite technically being linked to individual waterbodies for this analysis. Additionally, owing to restrictions of the NHD, surface area size cutoffs of the data, and the generally and notoriously poor ability to remotely sense small waterbody features in areas like mountains, this sample cannot represent an accurate count of lakes on the landscapes themselves. The ecoregions framework supports systematic ecological classification and aided spatially delineating USA mountain ranges. In instances where a lake boundary occurred in multiple ecoregions, and thus duplication occurred, the duplicate was removed. Lakes were assigned elevation data with {elevatr} (version 0.99.0) (Hollister et al. 2023).

High resolution (30 arc sec, ~1km) global downscaled air temperature data were acquired from the open access CHELSA climate database (Climatologies at High resolution for the Earth's Land Surface Areas; Version 2.1) (Karger et al. 2017, 2018, 2020). Mean daily air temperatures (TAS air temperatures at 2 meters from hourly ERA5 data) were acquired for both historical (1979–2019) and projected (2011–2040, 2041–2070, 2071–2100) time periods at the lowest provided resolution (monthly). The "business as usual" projected climatology (SSP 3 / RCP 7.0) was selected for being the most realistic and policy-relevant scenario to achieve the goal of assessing heat accumulation in mountain lake landscapes. Historical data were available in unique year–month combinations (e.g., per lake, n = 456), but projected data, as is typical of climatologies, were available only as a conglomerative average across each time period–month for each unique SSP scenario (e.g., per lake, n = 12 for the 2011–2041 time period under SSP 3). The year 1979 was excluded from analyses due to incomplete data. Lake data from the NHD were joined to CHELSA data to acquire watershed-level air temperature values at the landscape level; this allowed for fine-scale assessment of landscape temperature change; however the method remains relatively limited in granularity (i.e., a large lake and adjacent pond are not comparable, and empirical measurements at these locations may show greater variability), thus we do not extend our interpretations to the site-specific scale for this analysis.

Heat Accumulation

This study applies the Growing Degree Day (GDD) and Killing Degree Day (KDD) thermal metrics to translate changes in temperature in the mountain lake landscape into ecologically meaningful interpretations. As the analysis focuses on the lake landscape, we do not suggest air temperature is a substitute for water temperature nor do result interpretations require it. Both GDD and KDD are heat accumulation measures that have been broadly used for >70 years in ecology and >270 years in agronomy (Barnard 1948; Seamster 1950; Wilsie and Shaw 1954; Neuheimer and Taggart 2007; Butler and Huybers 2015). While GDD and KDD are related, they have divergent ramifications for organisms. GDD measures cumulative heat units above a base threshold temperature, typically a threshold for growth and development (Seuffert et al. 2012; Butler and Huybers 2015; Honsey et al. 2023). In contrast, KDD measures cumulative units over a known lethal temperature threshold and is used to help assess cumulative risk of severe heat exposure to organisms. KDD is a related metric to those used in heatwave studies (e.g., Tassone and Pace 2024) but emphasizes total accumulated heat as opposed to heat pulses. While GDD has long been applied as an ecological indicator in agricultural studies, it is generally underutilized in limnology and the aquatic sciences (Neuheimer and Taggart 2007; but see Venturelli et al. 2010; Rypel 2014a; Spurgeon et al. 2020; Mushegian et al. 2021). Only relatively recently has the GDD concept been integrated into studies relating to zooplankton and phytoplankton (Gillooly 2000; Dupuis and Hann 2009; Ralston et al. 2014), macrophytes (Beck et al. 2014), and freshwater bivalves (Watanabe et al. 2021).

This study quantified GDD and KDD metrics for mountain lake landscapes in both historical and projected time periods (**Figure 1**; **Figure S2-S3**). We calculated GDD for each unique *Lake–Year–Month* combination by adapting the standard degree days (DD) formula to:

$$DD = \sum_{t=1}^{N} T_t - T_0 \, , T_t > T_0$$

where N = number of days, T_t = mean temperature on a day t, and T_0 = threshold temperature beneath which thermal energy is considered negligible toward physiological growth and maturity processes of species in mountain lake landscapes, particularly aquatic species. To fit the structure of the data available for this study, we used the secondary equation and modified the following elements: N = number of months; T_t = mean temperature on a month t.

We used -5, 0, 5, and 10ºC as T_0 thresholds to explore trends. Ultimately, a GDD threshold of 0ºC was used because this was identified as the most parsimonious base temperature in general analyses of fish growth (Honsey et al. 2023). We calculated KDD using the same equation but used the 90% quantile for each mountain range (13.25 – 22.85 ºC) as the T_0 threshold temperature. KDDs therefore represent lake landscape temperatures that are, for native cold-adapted organisms at least, either lethal, near-lethal, or otherwise supraoptimal, leading to adverse effects on the organism's growth, performance, metabolic rates, etc.

In the event negative degree days resulted, these data were converted to zeros as it meant no heat had been accrued above the threshold. Observations where GDD=0 or KDD=0 were retained in the dataset for modeling (see Methods "Linear mixed-effect models"), but were removed from figures to improve data visualization. As CHELSA climate data were only available for unique *Year–Month* combinations, these data were expanded to complete the GDD or KDD calculation using mean monthly temperature as the expander for each month. Therefore, each day of a unique *Lake–Year*'s month received the same average temperature for each day of that respective month (Rypel 2012b, 2015). Last, these expanded values were summed for every unique *Lake–Year* to acquire the number of growing or killing degree days for a watershed location in a year.

Velocity of Climate Change

We measured velocity of change using {*lmerTest::lmer*} to run linear mixed effect models (Kuznetsova et al. 2017). In the models, the estimates optimized the "restricted maximum likelihood" (REML) criterion, *GDD* for each *Lake-Year* combination was the response variable, *Year* was a fixed effect, and *Lake* was a random effect (**Table S2**). The random effect slopes were subsequently interpreted as the velocity of change for each watershed. Overall trends in GDD were plotted with a parent regression line and random effect slopes examined as a function of elevation for each mountain range (**Figure 2-3**). Using GDD slopes, we additionally show differences in the velocity of change for each mountain range (**Figure 4**). A parallel analysis was performed using annual mean temperature (ºC) rather than GDD, and because similar trends resulted, we display only results from GDD for consistency with KDD analyses (**Figure S4-S5**). Both model response variables were transformed, GDD *ln(x+1)* or temperature *log(x+10)*, prior to modeling. The *log(x+10)* transformation was used to render all temperature values positive prior to taking the logarithm.

Climate Vulnerability Classification

We performed a k-means cluster analyses based on mean historical heat accumulation for a site (Mean GDD, *ln(x+1)* transformed) to identify and group lake landscapes within each mountain range based on similar vulnerability properties. K-means is an ideal method for classifying rate of change in climate data as the method is versatile, guarantees model convergence, is scalable and computationally efficient with large datasets, and is simple and readily interpretable (Rypel et al. 2019a) (**Figure 5; Figure S6**). The classification was *a priori* constrained to three clusters (i.e., cold, transitional, or hot). We elected not to cluster based on model slopes, primarily because the variance structure of projected climate data did not match that of the historical datasets. Hence given low sample size of projected data, and because GDD and slope are nearly colinear, we conservatively limited our analyses of slope to only historical data.

Climate Change Projections

We performed Discriminant Function Analyses (DFAs) to predict probability of lake assignment to one of the aforementioned clusters for three future time periods under the SSP 3 (RCP 7.0) climate scenario (**Table 1; Table S3**). Each lake landscape's mean historic GDD, and its respective cluster assignment, was used to build a predictive model for each mountain range separately. The continuous model variable, GDD, was $ln(x+1)$ transformed as in the k-means cluster analysis, and scaled. Projected GDD for each mountain range was used to aid in cluster predictions. Analyses were performed using the linear DFA function from the {MASS} package (version 7.3-60.0.1) (Venables and Ripley 2002). DFAs used to predict each ranges' future cluster assignments possessed a high degree of accuracy (>94%; **Table S3**). Using the above approach, we were able to successfully examine how climate vulnerability classifications changed given probable climate futures.

Data & Code Availability

Data materials used to construct this analysis are based on publicly available data cited in the manuscript text (i.e., NHD, Omernik, and CHELSA). Code to produce the main analysis are available on GitHub (https://github.com/caparisek/mtn_landscape_heat_accumulation) and are registered on Zenodo (https://doi.org/10.5281/zenodo.14954679).

Results

Statistical distributions in number and physical characteristics of individual lakes vary dramatically across the study mountain ranges (**Figure S1; Table S1**). For instance, mountain ranges like the Appalachians and Rockies have numerically many more lakes compared with other ranges. These ranges, as well as the Sierra Nevada, also have more lakes with smaller surface area compared to larger ones, yet in contrast to these three ranges, ranges like the Appalachians have numerically many more low elevation lakes overall as the Appalachians are a relatively lower mountain range in general. Understanding the distribution of lakes across mountain ranges is primarily limited by the capacity of remote sensing tools to detect all small lakes (Richardson et al. 2022). Nonetheless, with the data available, we observe lake surface area distributions of all mountain ranges are decidedly right-skewed, to varying degrees (**Table S1**). Trends in kurtosis (i.e., distribution tailedness) also shed light on how rare large lake ecosystems (e.g., Lake Tahoe, 496.2 km^2) are across mountain ranges. While all ranges exhibit leptokurtic distributions (i.e., kurtosis > 3, sharp peak in small lakes with long, thin tails toward larger lakes), the degree to which they exhibit this varies greatly.

Heat Accumulation

In all mountain ranges, mean growing degree days (GDD) and killing degree days (KDD) increased over the historical period (1980–2019), and from the historical baseline to 2100 in the projected SSP 3 (RCP 7.0) climate scenario (**Figure 1**). Based on downscaled historical climate data, lakes in low elevation watersheds are consistently exposed to a greater number of GDDs than high elevation lakes; this pattern was present in all mountain ranges (**Figure S2**). Methodologically, the KDD threshold was unique for each mountain range, and interestingly, a range of mid-high elevation sites experience low KDD with sites at lower elevations often having the highest KDDs. In some cases, there was a tight relationship between elevation and KDD (e.g., Sierra Nevada, Blue Ridge), but in others, the relationship was more heterogenous (e.g., Cascades, Rockies). Similar heat accumulation trends, and an increase in KDD over time, are also evident in the future (**Figure S3**). Quantiles derived from historical climate data illustrate the distributions of air temperatures within these diverse lake landscapes (Median = 4.75^{o}C, Interquartile Range = -3.15 – 12.95^{o}C).

Velocity of Climate Change

Mixed-effect models examining relationships between historical year and GDD (heat accumulation) revealed increasing trends in every mountain range ($R^2_c > 0.89$ (i.e., R^2_c is the variance explained by both fixed and random effects relative to total variance); **Table S2; Figure 2**). This pattern was almost identical for models constructed using annual mean temperature (^{o}C) in place of GDD (**Figure S4**). Slopes extracted from these models for each site (as random effects), allowed comparisons of velocity of change estimates across sites. For both GDD and temperature models, and across all mountain ranges, velocities of change correlated significantly with elevation (**Figure 3; Figure S5;** Pearson's R Correlations: all correlations -0.48 – -0.95, all p-values < 0.0001). Thus, lake landscapes with the highest velocity of climate warming tended to be those distributed at lower elevations.

Boxplots examining GDD-modeled slope as a function of mountain range indicate which lake landscapes experience faster rates of change than others. For example, the Wasatch-Uinta, Idaho Batholith, Arizona-New Mexico, and Sierra Nevada Ranges are changing most quickly, while the Blue Ridge, Klamath, and Appalachian Ranges appear to be changing relatively more slowly (**Figure 4**).

Climate Vulnerability Classification

We built a climate change vulnerability classification using hindcasted air temperature heat accumulation data spanning a 38 y time series. Thus, every modeled mountain lake landscape was identified and subsequently its lake-watershed sites clustered into one of three classes of climate vulnerability: (1) cold, (2) transitional, or (3) hot (**Figure 5; Figure S6**). Across all mountain ranges 1980–2019, 19% of sites hold characteristics consistent with high heat and fast rates of heat accumulation, 42% of sites remain colder with slow rates of change, and 39% of sites are classified as transitional (**Table 1**). The percentage of watersheds assigned to each of these categories varied for each mountain range, such that historically the Sierra Nevada had 68% of its watersheds classified as cold, and Idaho Batholith, Wasatch-Uinta, and the Appalachians had 48%, 47%, and 45%, respectively. In contrast, ranges such as Blue Ridge and Arizona-New Mexico had 22-25% of watersheds classified as cold. However, these proportions change dramatically over time with probable climate projections (*see Climate Change Projections below*).

Climate Change Projections

Discriminant Function Analyses (DFAs) for each mountain range performed exceptionally well ($> 94\%$ accuracy, $p < 0.0001$; **Table S3**). DFAs revealed that by the end of the century just 8% of sites across all ranges will be classified as cold, 33% of sites will likely be classified as hot, and 59% of sites will be transitional (**Table 1**). This represents changes of -82%, +80%, and +51%, respectively, from the historical baseline. Ranges such as Blue Ridge, Idaho Batholith, and Klamath, are anticipated to have just 1% of "cold" lake landscapes left by the end of the century, with the Appalachians, Cascades, Rockies, and Wasatch-Uinta having just 8%, 7%, 7%, and 6% of cold landscapes remaining (**Figure 4**).

Discussion

Landscape differences in geology, latitude, and longitude promote differences in the ecology of lakes (Medeiros et al. 2012; Read et al. 2015). In this study we (i) quantified heat accumulation and velocity of change across mountain lake landscapes in the USA and found that lower elevation landscapes, and those with greatest historical velocities of change, are most vulnerable. Further, the percent of mountain watersheds classified as highly vulnerable is anticipated to jump from 19% to 33% by the year 2100. Additionally, we (ii) investigated the potential of applying the agro-climate thermal time indicator, *killing degree days*, specifically to watersheds and aquatic ecosystems, and found that the percent change in mean killing degree days will increase, on average, by 236% by the year 2100. We also (iiI) created a climate change vulnerability framework to assist decision makers in the allocation of their limited conservation resources towards these sensitive environments.

Thermal extremes in freshwaters are increasing in frequency and threaten aquatic organisms and ecological processes as end-of-century approaches (Becker et al. 2018; Till et al. 2019; DuBose et al. 2019). In high-altitude ecosystems especially, snowpack is diminishing and ice-cover on lakes is reducing rapidly; the ramifications of which alter water security downstream and wreak havoc on thermal regimes in these coldwater habitats (Viviroli et al. 2011; Sadro et al. 2019; Moser et al. 2019; Jane et al. 2024). Higher heat accumulation in lakes is also known to increase disease susceptibility (Marcogliese 2008), favor phytoplankton blooms

(Piccioni et al. 2021), modify lake stratification dynamics (Woolway et al. 2021), and reduce oxygen levels in lakes (Blumberg and Di Toro 1990; Bukaveckas et al. 2023), all of which could disrupt or rewire food webs (Bartley et al. 2019). Populations of a species that experience different levels of temperature variation across a landscape will likely develop different thermal tolerances and have altered thermal ranges over time (Gill et al. 2016; Shah et al. 2017; Polato et al. 2018). Some taxa, like some lake-dwelling mountain aquatic insects, may be able to mitigate risk of heat exposure in lakes by migrating to cooler refugia (e.g., spring- or snowpack-fed streams) if required (Birrell et al. 2020; Parisek et al. 2023). However, other taxa may be unable to effectively disperse to more favorable habitats, especially if lakes are not hydrologically connected, and so both dispersal ability and the landscape-specific context of lakes will be important in determining ultimate changes in diversity.

In this study, we predict mountain lake landscapes that previously supported more favorable coldwater habitats will experience more days with higher temperatures, greater accumulated heat, and an amplification of killing heat. Where lake landscapes newly experience greater growing degree days, these warmer temperatures may open up novel habitats suitable to support optimal growth and development in the future. However, we also predict these landscapes will experience 215 –254% (mean = 236%) increases in heat accumulation exceeding the 90th percentile historical temperatures. Our findings suggest that across USA mountain ranges, watersheds positioned at lower elevations are consistently exposed to higher rates of heat accumulation. This latter point, despite being based on air temperature data, is also supported by observed trends in surface water temperature from some mountain ranges, such as the Pyrenees (Sabás et al. 2021). The accumulated heat (i.e., degree-day) metric is a valuable tool for assessing changing heat content dynamics (Choiński et al. 2015; Christianson et al. 2019). In freshwater systems generally, increased heat accumulation extends the duration of the growing season and can enhance maturation rate in fishes (Venturelli et al. 2010; Uphoff et al. 2013); however, some fish populations have lower tolerance to high temperatures and, consequently, perform less well (McDermid et al. 2013; Feiner et al. 2016). Indeed, research suggests ecological response to increased heat accumulation is nonlinear, as it is also known to be ecosystem-specific and heavily associated with changes in latitude (Rypel 2012a; Richard and Rypel 2013; Rypel and David 2017; Spurgeon et al. 2020). It is unknown how fishes and other aquatic organisms respond to heat accumulation along an elevation gradient. For instance, organisms may attempt to migrate or else attempt to tolerate warming temperatures. Relatedly, climate change may simultaneously increase primary productivity and thereby improve food resources for higher order taxa in the food web.

Quantifying geographically distinct velocities of climate change provides critical insight and nuance on the uneven impacts of climate change. For example, we observe that velocity of climate change varies considerably by mountain range (i.e., some ranges experience greater velocities of change through time, while others have relatively slower rates of heat accumulation). This finding provides key insight on the fragility of certain regions and lakes to ecosystem state shifts (Scheffer 1990; Scheffer and Carpenter 2003; Butitta et al. 2017). Individual species and ecosystems possess different thresholds for how they will react to higher heat accumulation; however, the pace at which they can acclimatize to the rapidity of these changes is also important. Species with less time to adjust to rapidly increasing temperatures (e.g., long-lived and less mobile organisms), are likely to struggle in climates whose heat accumulation occurs at a higher velocity (Pacheco-Riaño et al. 2023; Rypel 2023). However a slow rate of change can also be dangerous, especially in regions where climate variance has historically been low (Kraemer et al. 2015). Likewise, populations of a species experiencing thermal variability will have differing thermal ranges (Gill et al. 2016; Shah et al. 2017; Polato et al. 2018).

While GDD and velocity of change are closely linked, the relationships are apparently often curvilinear (e.g., Appalachians, Cascades, Sierra Nevada; **Figure 5**). Therefore, velocity of change actually slows once a threshold of high heat accumulation is reached. This pattern is consistent with expectations from regime shift theory, where the highest rates of change are more frequently observed in systems undergoing a state shift (Butitta et al. 2017). Combined, the empirical patterns in velocity of thermal change suggests these landscapes have likely been rapidly shifting for some time, so much so perhaps, that the rate of change is actually beginning to slow. These relationships importantly highlight how heat accumulation and velocity of change are fundamentally different assessments of vulnerability that can sometimes, though not always, be correlated with one another (Hamann et al. 2015; Woolway and Maberly 2020; Woolway 2023). Some of our study mountain ranges showed parallel results in their heat accumulation and velocity of climate change (e.g., Wasatch-Uinta Mountains) while in others, heat accumulation and velocity of climate change were decoupled (e.g., Klamath Mountains). Therefore, conservation applications based on just one or the other may come to divergent conclusions. Coupling velocity of change with heat accumulation provides a richer portrait of vulnerability, which may be of interest in future climate change assessments efforts going forward.

A limitation of our analysis is the lack of available water temperature data, a problem that is exacerbated by the lack of study in mountain systems more generally. These data are not yet feasible to acquire at scale, and so here we used air temperature data to explore changing patterns in accumulated heat in the lake landscape. There is evidence that lake surface water temperature

(LSWT) does generally correspond closely with air temperatures (Armitage 2023) and thus can still be a useful proxy, specifically for non-taxa-specific landscape-level temperature-based analyses. While LSWT cannot serve as a proxy for lake temperature at depth, and attaining lake depth temperature estimates at scale remains elusive to scientists, this information still provides valuable insights into microclimates experienced in mountain lake watersheds. Future work could build from this study by forging models on well-studied lakes that generate hindcasted and forecasted lake temperatures (Read et al. 2019; Willard et al. 2021) rather than just lake landscapes, or applying statistical correction factors.

It is worth noting that lakes themselves do not necessarily show the same temperature trends as their watersheds, and thus these results should only be interpreted as landscape-level trends. As demonstrated by **Figure S1** and **Table S1**, while most mountain ranges are indeed skewed toward having smaller waterbodies, large outlier lakes are also present (e.g., Lake Tahoe, in the Sierra Nevada mountains). Factors contributing to the lake heat budget, such as duration of ice cover, the water color and the resulting attenuation coefficient of radiation, lake morphology such as surface area and volume, and exposure to solar radiation, cloud cover, and albedo effects, play key roles in making lake warming not a geographically consistent phenomena (O'Reilly et al. 2015). Additionally, while high elevation mountain lakes may experience greater elevation-dependent warming throughout the day, reduced snow cover in a given year coupled with greater solar radiation will drive convective cooling (i.e., night time heat loss) which plays a large role in the actual water temperatures in mountain lakes. Seasonal effects, such as the ice-free season leading to more warming in the summer and ice and snow cover enhancing colder temperatures in the winter, also play significant roles in mountain lake temperatures (Hampton et al. 2017). Thus, even though mountain lakes should be experiencing high rates of elevation dependent warming, factors such as the timing and volume of snow melt, the duration of the ice-free season, and the magnitude of convective nighttime cooling all can play important roles in lake heat budgets, causing lakes to warm at rates slower than would be expected. Finally, we note the relationship between lake surface area and elevation is quite varied across the ranges (**Figure S1, Panel D**). This variation would likely present differences in lake heat budgets as well. This area of research would benefit from having the ability to tease apart nuances such as lake volume, maximum depth, morphology, and convective cooling, as these could all reasonably influence the speed at which lakes accumulate heat as landscape temperatures rise (Sabás et al. 2021).

Ecosystem vulnerability assessments are core to advancing conservation activities at many scales (Schupp 1992; Wehrly et al. 2012; Rypel et al. 2019b; Giuliani et al. 2019). The goal of our proposed climate change classification is to help identify, across multiple mountain ranges, the vulnerability of individual mountain lake landscapes to increasing heat accumulation. The three clustering tiers are delineated by (1) low heat accumulation, often with sites from high-elevation; (2) transitional, often with sites from mid-elevation; and (3) high heat accumulation, often with sites from lower elevation ranges. Combined, the classification schema shows lower-elevation mountain lakes are experiencing more rapid landscape-level thermal change across all USA mountain ranges. These lakes are also most likely to first experience increased killing degree days as end of the century approaches. Further, our findings suggest particular conservation consideration should be given to watersheds where cold-adapted endemic species have fewer than 5% of cool landscape available to them by the end of the century (e.g., Appalachians, Blue Ridge, Idaho Batholith, Klamath).

Accelerating change in freshwater systems will force managers to strategically select where they can reasonably work for maximal impact. The vulnerability schema provided here provides an initial tool to help. Global lake thermal regimes are already undergoing worldwide shifts at increasing velocities (Maberly et al. 2020; Woolway and Maberly 2020). No study exists, however, which classifies lake landscape vulnerability in mountain regions for anticipated heat accumulation and rates of change. Previous accepted frameworks for lake thermal classification exist, although they emphasize mixing regimes and require specific data to perform multi-dimensional lake models (Hutchinson and Löffler 1956; Lewis Jr. 1983; Woolway and Merchant 2019). To assess lake landscape vulnerability at scale, however, these data are not available and thus application of these frameworks are limited. Numerous assessments have sought to quantify vulnerability of lakes, depending on the focal need of the assessment, including through change in eutrophication (Giuliani et al. 2019), pollution resilience (Wu et al. 2012), water balance (Bracht-Flyr et al. 2013), and invertebrate-based temperature reconstructions (Eggermont et al. 2010). Some studies have concluded high-elevation lakes to be most vulnerable to change when specifically focusing on changes in ice dynamics, which low elevation lakes do not frequently experience (Gądek et al. 2020; Råman Vinnå et al. 2021). However assessments using the accumulated degree-day approach supports our finding that low-elevation watersheds are indeed highly sensitive to warming trends (Thompson et al. 2005; Sabás et al. 2021).

There are several potential uses for our mountain lake landscape classification framework. Many of the most well-studied mountain lakes are located at relatively high elevations in their mountain ranges. Results from this study suggest managers should increasingly monitor coldwater lakes at lower-to-mid elevations. Further, while shallow versus deep lakes would be affected on the lake landscape differently, these watershed locations still are mostly likely to experience the greatest accumulated landscape heat. Regional managers can use our classification to identify specific watersheds of greatest threat to loss of endemic species. Further, the classification provides an initial ability to better understand types of challenges these species are uniquely facing (e.g., fast change or a "slow boil") and thus provides an ability for managers to take early action in watersheds undergoing the greatest volume of threats. Yet whereas climate change itself is unmanageable at a local scale, conservation practitioners must find ways of building resilience into ecosystems using the levers that they do have control over (Rypel and Magnuson 2019). For some watersheds, this might mean reduced harvest limits or improved in-lake or shoreline habitats (Carpenter et al. 2017). In other ecosystems, it may entail improved management of the watershed, land use and nutrient loading (Jacobson et al. 2016; Lau et al. 2022; Jane et al. 2024). We therefore encourage managers to use the information provided here to plan resource allocation, funding needs, and decision making towards climate change resilience.

Freshwater biodiversity is increasingly challenged by the scope and extent of global climate change and human domination of the world's water cycle (Reid et al. 2019; Tickner et al. 2020; Flitcroft et al. 2023). This analysis provides an initial attempt and novel perspective to understand lake landscape vulnerability across USA mountain ranges. Our results show how vulnerable mountain lakes are experiencing unprecedented exposures to heat accumulation, especially at low elevations. Increased velocities of change are also fundamentally reshaping the structure and function of these ecosystems and increasing their frailty. Conservation managers need tools to prioritize their time, energy, personnel, and budget. In providing this classification and vulnerability analysis of the USA mountain lake landscapes, we hope to deliver one useful tool for aiding in complicated decision-making processes. Overall, our results call attention to the wide ways in which mountain lake landscapes are likely to change in the next 75 years.

References

Abbasi, A. O., C. W. Woodall, J. G. P. Gamarra, C. Hui, N. Picard, T. Ochuodho, S. de-Miguel, R. Sahay, S. Fei, A. Paquette, H. Y. H. Chen, A. C. Catlin, and J. Liang. 2024. Forest types outpaced tree species in centroid-based range shifts under global change. Frontiers in Ecology and Evolution 12.

Adrian, R., C. M. O'Reilly, H. Zagarese, S. B. Baines, D. O. Hessen, W. Keller, D. M. Livingstone, R. Sommaruga, D. Straile, E. Van Donk, G. A. Weyhenmeyer, and M. Winder. 2009. Lakes as sentinels of climate change. Limnology and Oceanography 54(6part2):2283–2297.

Alexander, J. M., J. M. Diez, and J. M. Levine. 2015. Novel competitors shape species' responses to climate change. Nature 525(7570):515–518.

Armitage, D. W. 2023. Global maps of lake surface water temperatures reveal pitfalls of air-for-water substitutions in ecological prediction. Ecography 2023(2):e06595.

Balik, J. A., H. S. Greig, B. W. Taylor, and S. A. Wissinger. 2023. Consequences of climate-induced range expansions on multiple ecosystem functions. Communications Biology 6(1):1–9.

Barnard, J. D. 1948. Heat units as a measure of canning crop maturity. The Canner 106(16):28.

Barnett, J., L. S. Evans, C. Gross, A. S. Kiem, R. T. Kingsford, J. P. Palutikof, C. M. Pickering, and S. G. Smithers. 2015. From barriers to limits to climate change adaptation: path dependency and the speed of change. Ecology and Society 20(3).

Baron, J. S., N. L. Poff, P. L. Angermeier, C. N. Dahm, P. H. Gleick, N. G. Hairston Jr., R. B. Jackson, C. A. Johnston, B. D. Richter, and A. D. Steinman. 2002. Meeting Ecological and Societal Needs for Freshwater. Ecological Applications 12(5):1247–1260.

Bartley, T. J., K. S. McCann, C. Bieg, K. Cazelles, M. Granados, M. M. Guzzo, A. S. MacDougall, T. D. Tunney, and B. C. McMeans. 2019. Food web rewiring in a changing world. Nature Ecology & Evolution 3(3):345–354.

Beck, M. W., C. M. Tomcko, R. D. Valley, and D. F. Staples. 2014. Analysis of macrophyte indicator variation as a function of sampling, temporal, and stressor effects. Ecological Indicators 46:323–335.

Becker, L. A., S. A. Crichigno, and V. E. Cussac. 2018. Climate change impacts on freshwater fishes: a Patagonian perspective. Hydrobiologia 816(1):21–38.

Bender, I. M. A., W. D. Kissling, K. Böhning-Gaese, I. Hensen, I. Kühn, L. Nowak, T. Töpfer, T. Wiegand, D. M. Dehling, and M. Schleuning. 2019. Projected impacts of climate change on functional diversity of frugivorous birds along a tropical elevational gradient. Scientific Reports 9(1):17708.

Birrell, J. H., A. A. Shah, S. Hotaling, J. J. Giersch, C. E. Williamson, D. Jacobsen, and H. A. Woods. 2020. Insects in high-elevation streams: Life in extreme environments imperiled by climate change. Global Change Biology 26(12):6667–6684.

Blumberg, A. F., and D. M. Di Toro. 1990. Effects of Climate Warming on Dissolved Oxygen Concentrations in Lake Erie. Transactions of the American Fisheries Society 119(2):210–223.

Bonacina, L., F. Fasano, V. Mezzanotte, and R. Fornaroli. 2023. Effects of water temperature on freshwater macroinvertebrates: a systematic review. Biological Reviews 98(1):191–221.

Bracht-Flyr, B., E. Istanbulluoglu, and S. Fritz. 2013. A hydro-climatological lake classification model and its evaluation using global data. Journal of Hydrology 486:376–383.

Bukaveckas, P. A., L. Buikema, and C. Stewart. 2023. Effects of climate change and variability on thermal regime and dissolved oxygen resources of oligotrophic lakes in the Adirondack Mountain region. Aquatic Sciences 86(1):9.

Büntgen, U., L. Greuter, K. Bollmann, H. Jenny, A. Liebhold, J. D. Galván, N. C. Stenseth, C. Andrew, and A. Mysterud. 2017. Elevational range shifts in four mountain ungulate species from the Swiss Alps. Ecosphere 8(4):e01761.

Butitta, V. L., S. R. Carpenter, L. C. Loken, M. L. Pace, and E. H. Stanley. 2017. Spatial early warning signals in a lake manipulation. Ecosphere 8(10):e01941.

Butler, E. E., and P. Huybers. 2015. Variations in the sensitivity of US maize yield to extreme temperatures by region and growth phase. Environmental Research Letters 10(3):034009.

Carpenter, S. R., W. A. Brock, G. J. A. Hansen, J. F. Hansen, J. M. Hennessy, D. A. Isermann, E. J. Pedersen, K. M. Perales, A. L. Rypel, G. G. Sass, T. D. Tunney, and M. J. Vander Zanden. 2017. Defining a Safe Operating Space for inland recreational fisheries. Fish and Fisheries 18(6):1150–1160.

Carpenter, S. R., S. G. Fisher, N. B. Grimm, and J. F. Kitchell. 1992. Global Change and Freshwater Ecosystems. Annual Review of Ecology, Evolution and Systematics 23(1):119–139.

Choiński, A., M. Ptak, and A. Strzelczak. 2015. Changeability of Accumulated Heat Content in Alpine-Type Lakes. Polish Journal of Environmental Studies 24(6):2363–2369.

Christianson, K. R., B. M. Johnson, M. B. Hooten, and J. J. Roberts. 2019. Estimating lake–climate responses from sparse data: An application to high elevation lakes. Limnology and Oceanography 64(3):1371–1385.

Collen, B., F. Whitton, E. E. Dyer, J. E. M. Baillie, N. Cumberlidge, W. R. T. Darwall, C. Pollock, N. I. Richman, A.-M. Soulsby, and M. Böhm. 2014. Global patterns of freshwater species diversity, threat and endemism. Global Ecology and Biogeography 23(1):40–51.

Collins, S. L., M. L. Avolio, C. Gries, L. M. Hallett, S. E. Koerner, K. J. La Pierre, A. L. Rypel, E. R. Sokol, S. B. Fey, D. F. B. Flynn, S. K. Jones, L. M. Ladwig, J. Ripplinger, and M. B. Jones. 2018. Temporal heterogeneity increases with spatial heterogeneity in ecological communities. Ecology 99(4):858–865.

DuBose, T. P., C. L. Atkinson, C. C. Vaughn, and S. W. Golladay. 2019. Drought-Induced, Punctuated Loss of Freshwater Mussels Alters Ecosystem Function Across Temporal Scales. Frontiers in Ecology and Evolution 7.

Dupuis, A. P., and B. J. Hann. 2009. Warm spring and summer water temperatures in small eutrophic lakes of the Canadian prairies: potential implications for phytoplankton and zooplankton. Journal of Plankton Research 31(5):489–502.

Eggermont, H., D. Verschuren, L. Audenaert, L. Lens, J. Russell, G. Klaassen, and O. Heiri. 2010. Limnological and ecological sensitivity of Rwenzori mountain lakes to climate warming. Hydrobiologia 648(1):123–142.

Feiner, Z. S., H.-Y. Wang, D. W. Einhouse, James. R. Jackson, E. S. Rutherford, C. Schelb, C. S. Vandergoot, T. G. Zorn, and T. O. Höök. 2016. Thermal environment and maternal effects shape egg size in a freshwater fish. Ecosphere 7(5):e01304.

Ficke, A. D., C. A. Myrick, and L. J. Hansen. 2007. Potential impacts of global climate change on freshwater fisheries. Reviews in Fish Biology and Fisheries 17(4):581–613.

Flitcroft, R. L., R. Abell, I. Harrison, I. Arismendi, and B. E. Penaluna. 2023. Making global targets local for freshwater protection. Nature Sustainability 6(12):1499–1502.

Gądek, B. A., B. J. Szypuła, and M. Szumny. 2020. Classification of the Tatra Mountain lakes in terms of the duration of their ice cover (Poland and Slovakia): Ice cover classification of the Tatra Mountain lakes. Journal of Limnology 79(1).

Gill, B. A., B. C. Kondratieff, K. L. Casner, A. C. Encalada, A. S. Flecker, D. G. Gannon, C. K. Ghalambor, J. M. Guayasamin, N. L. Poff, M. P. Simmons, S. A. Thomas, K. R. Zamudio, and W. C. Funk. 2016. Cryptic species diversity reveals biogeographic support for the 'mountain passes are higher in the tropics' hypothesis. Proceedings of the Royal Society B: Biological Sciences 283(1832):20160553.

Gillooly, J. F. 2000. Effect of body size and temperature on generation time in zooplankton. Journal of Plankton Research 22(2):241–251.

Giuliani, C., A. C. Veisz, M. Piccinno, and F. Recanatesi. 2019. Estimating vulnerability of water body using Sentinel-2 images and environmental modelling: the study case of Bracciano Lake (Italy). European Journal of Remote Sensing 52(sup4):64–73.

Greig, H. S., P. Kratina, P. L. Thompson, W. J. Palen, J. S. Richardson, and J. B. Shurin. 2012. Warming, eutrophication, and predator loss amplify subsidies between aquatic and terrestrial ecosystems. Global Change Biology 18(2):504–514.

Hamann, A., D. R. Roberts, Q. E. Barber, C. Carroll, and S. E. Nielsen. 2015. Velocity of climate change algorithms for guiding conservation and management. Global Change Biology 21(2):997–1004.

Hampton, S. E., A. W. E. Galloway, S. M. Powers, T. Ozersky, K. H. Woo, R. D. Batt, S. G. Labou, C. M. O'Reilly, S. Sharma, N. R. Lottig, E. H. Stanley, R. L. North, J. D.

Stockwell, R. Adrian, G. A. Weyhenmeyer, L. Arvola, H. M. Baulch, I. Bertani, L. L. Bowman Jr., C. C. Carey, J. Catalan, W. Colom-Montero, L. M. Domine, M. Felip, I. Granados, C. Gries, H.-P. Grossart, J. Haberman, M. Haldna, B. Hayden, S. N. Higgins, J. C. Jolley, K. K. Kahilainen, E. Kaup, M. J. Kehoe, S. MacIntyre, A. W. Mackay, H. L. Mariash, R. M. McKay, B. Nixdorf, P. Nõges, T. Nõges, M. Palmer, D. C. Pierson, D. M. Post, M. J. Pruett, M. Rautio, J. S. Read, S. L. Roberts, J. Rücker, S. Sadro, E. A. Silow, D. E. Smith, R. W. Sterner, G. E. A. Swann, M. A. Timofeyev, M. Toro, M. R. Twiss, R. J. Vogt, S. B. Watson, E. J. Whiteford, and M. A. Xenopoulos. 2017. Ecology under lake ice. Ecology Letters 20(1):98–111.

Hollister, J., T. Shah, J. Nowosad, A. Robitaille, M. Beck, and M. Johnson. 2023. elevatr: Access Elevation Data from Various APIs. doi:10.5281/zenodo.8335450, R package version 0.99.0, https://github.com/jhollist/elevatr/.

Honsey, A. E., A. L. Rypel, and P. A. Venturelli. 2023. Guidance for selecting base temperatures when using degree-days in fish growth analyses. Canadian Journal of Fisheries and Aquatic Sciences 80(3):549–562.

Hutchinson, G. E., and H. Löffler. 1956. The thermal classification of lakes. Proceedings of the National Academy of Sciences 42(2):84–86.

Inouye, D. W. 2020. Effects of climate change on alpine plants and their pollinators. Annals of the New York Academy of Sciences 1469(1):26–37.

Jacobson, P. C., T. K. Cross, D. L. Dustin, and M. Duval. 2016. A Fish Habitat Conservation Framework for Minnesota Lakes. Fisheries 41(6):302–317.

Jane, S. F., T. M. Detmer, S. L. Larrick, K. C. Rose, E. A. Randall, K. J. Jirka, and P. B. McIntyre. 2024. Concurrent warming and browning eliminate cold-water fish habitat in many temperate lakes. Proceedings of the National Academy of Sciences 121(2):e2306906120.

Jeppesen, E., M. Meerhoff, K. Holmgren, I. González-Bergonzoni, F. Teixeira-de Mello, S. A. J. Declerck, L. De Meester, M. Søndergaard, T. L. Lauridsen, R. Bjerring, J. M. Conde-Porcuna, N. Mazzeo, C. Iglesias, M. Reizenstein, H. J. Malmquist, Z. Liu, D. Balayla, and X. Lazzaro. 2010. Impacts of climate warming on lake fish community structure and potential effects on ecosystem function. Hydrobiologia 646(1):73–90.

Karger, D. N., O. Conrad, J. Böhner, T. Kawohl, H. Kreft, R. W. Soria-Auza, N. E. Zimmermann, H. P. Linder, and M. Kessler. 2018. Data from: Climatologies at high resolution for the earth’s land surface areas. EnviDat. https://doi.org/10.16904/envidat.228.v2.1.

Karger, D. N., O. Conrad, J. Böhner, T. Kawohl, H. Kreft, R. W. Soria-Auza, N. E. Zimmermann, P. Linder, and M. Kessler. 2017. Climatologies at high resolution for the Earth land surface areas. Scientific Data 4:170122.

Karger, D. N., B. Dabaghchian, S. Lange, W. Thuiller, N. E. Zimmermann, and C. H. Graham. 2020. High resolution climate data for Europe. EnviDat. http://dx.doi.org/doi:10.16904/envidat.150.

Knouft, J. H., and D. L. Ficklin. 2017. The Potential Impacts of Climate Change on Biodiversity in Flowing Freshwater Systems. Annual Review of Ecology, Evolution, and Systematics 48(Volume 48, 2017):111–133.

Kraemer, B. M., O. Anneville, S. Chandra, M. Dix, E. Kuusisto, D. M. Livingstone, A. Rimmer, S. G. Schladow, E. Silow, L. M. Sitoki, R. Tamatamah, Y. Vadeboncoeur, and P. B.

McIntyre. 2015. Morphometry and average temperature affect lake stratification responses to climate change. Geophysical Research Letters 42(12):4981–4988.

Kratz, T., K. Webster, C. Bowser, J. Maguson, and B. Benson. 1997. The influence of landscape position on lakes in northern Wisconsin. Freshwater Biology 37(1):209–217.

Kuefner, W., A. M. Hofmann, J. Geist, N. Dubois, and U. Raeder. 2021. Algal Community Change in Mountain Lakes of the Alps Reveals Effects of Climate Warming and Shifting Treelines1. Journal of Phycology 57(4):1266–1283.

Kuznetsova, A., P. Brockhoff, and R. Christensen. 2017. lmerTest Package: Tests in Linear Mixed Effects Models. Journal of Statistical Software 82(13):1–26.

Larsen, S., J. D. Muehlbauer, and E. Marti. 2016. Resource subsidies between stream and terrestrial ecosystems under global change. Global Change Biology 22(7):2489–2504.

Lau, D. C. P., K. S. Christoffersen, J. Erkinaro, B. Hayden, J. Heino, S. Hellsten, K. Holmgren, K. K. Kahilainen, M. Kahlert, S. M. Karjalainen, J. Karlsson, L. Forsström, J. Lento, M. Mjelde, J. Ruuhijärvi, S. Sandøy, A. K. Schartau, M.-A. Svenning, T. Vrede, and W. Goedkoop. 2022. Multitrophic biodiversity patterns and environmental descriptors of sub-Arctic lakes in northern Europe. Freshwater Biology 67(1):30–48.

Ledger, M. E., L. E. Brown, F. K. Edwards, A. M. Milner, and G. Woodward. 2013. Drought alters the structure and functioning of complex food webs. Nature Climate Change 3(3):223–227.

Lewis Jr., W. M. 1983. A Revised Classification of Lakes Based on Mixing. Canadian Journal of Fisheries and Aquatic Sciences 40(10):1779–1787.

Lusardi, R. A., A. L. Nichols, A. D. Willis, C. A. Jeffres, A. H. Kiers, E. E. Van Nieuwenhuyse, and R. A. Dahlgren. 2021. Not All Rivers Are Created Equal: The Importance of Spring-Fed Rivers under a Changing Climate. Water 13(12):1652.

Lyons, J., T. Zorn, J. Stewart, P. Seelbach, K. Wehrly, and L. Wang. 2009. Defining and Characterizing Coolwater Streams and Their Fish Assemblages in Michigan and Wisconsin, USA. North American Journal of Fisheries Management 29(4):1130–1151.

Maberly, S. C., R. A. O'Donnell, R. I. Woolway, M. E. J. Cutler, M. Gong, I. D. Jones, C. J. Merchant, C. A. Miller, E. Politi, E. M. Scott, S. J. Thackeray, and A. N. Tyler. 2020. Global lake thermal regions shift under climate change. Nature Communications 11(1):1232.

Magnuson, J. J., L. B. Crowder, and P. A. Medvick. 1979. Temperature as an Ecological Resource. American Zoologist 19(1):331–343.

Mamantov, M. A., D. K. Gibson-Reinemer, E. B. Linck, and K. S. Sheldon. 2021. Climate-driven range shifts of montane species vary with elevation. Global Ecology and Biogeography 30(4):784–794.

Marcogliese, D. J. 2008. The impact of climate change on the parasites and infectious diseases of aquatic animals. Revue Scientifique Et Technique (International Office of Epizootics) 27(2):467–484.

McDermid, J. L., C. C. Wilson, W. N. Sloan, and B. J. Shuter. 2013. Intraspecific Differences in Thermal Biology among Inland Lake Trout Populations. Transactions of the American Fisheries Society 142(3):756–766.

Medeiros, A. S., R. G. Biastoch, C. E. Luszczek, X. A. Wang, D. C. G. Muir, and R. Quinlan. 2012. Patterns in the limnology of lakes and ponds across multiple local and regional environmental gradients in the eastern Canadian Arctic. Inland Waters 2(2):59–76.

Moser, K. A., J. S. Baron, J. Brahney, I. A. Oleksy, J. E. Saros, E. J. Hundey, S. Sadro, J. Kopáček, R. Sommaruga, M. J. Kainz, A. L. Strecker, S. Chandra, D. M. Walters, D. L. Preston, N. Michelutti, F. Lepori, S. A. Spaulding, K. R. Christianson, J. M. Melack, and J. P. Smol. 2019. Mountain lakes: Eyes on global environmental change. Global and Planetary Change 178:77–95.

Mushegian, A. A., N. Neupane, Z. Batz, M. Mogi, N. Tuno, T. Toma, I. Miyagi, L. Ries, and P. A. Armbruster. 2021. Ecological mechanism of climate-mediated selection in a rapidly evolving invasive species. Ecology Letters 24(4):698–707.

Nakano, S., H. Miyasaka, and N. Kuhara. 1999. Terrestrial–Aquatic Linkages: Riparian Arthropod Inputs Alter Trophic Cascades in a Stream Food Web. Ecology 80(7):2435–2441.

Neuheimer, A. B., and C. T. Taggart. 2007. The growing degree-day and fish size-at-age: the overlooked metric. Canadian Journal of Fisheries and Aquatic Sciences 64(2):375–385.

Omernik, J. M. 1995. Ecoregions: a framework for managing ecosystems. The George Wright Forum. George Wright Society. 12(1):35–50.

Omernik, J. M., and G. E. Griffith. 2014. Ecoregions of the conterminous United States: evolution of a hierarchical spatial framework. Environmental Management 54(6):1249–1266.

Pacheco-Riaño, L. C., F. Høistad Schei, S. G. A. Flantua, and J.-A. Grytnes. 2023. Lags in the response of plant assemblages to global warming depends on temperature-change velocity. Global Ecology and Biogeography 32(5):719–733.

Parisek, C. A., M. P. Marchetti, and M. R. Cover. 2023. Morphological plasticity in a caddisfly that co-occurs in lakes and streams. Freshwater Science 42(2):161–175.

Piccioni, F., C. Casenave, B. J. Lemaire, P. Le Moigne, P. Dubois, and B. Vinçon-Leite. 2021. The thermal response of small and shallow lakes to climate change: new insights from 3D hindcast modelling. Earth System Dynamics 12(2):439–456.

Piovia-Scott, J., S. Sadro, R. A. Knapp, J. Sickman, K. L. Pope, and S. Chandra. 2016. Variation in reciprocal subsidies between lakes and land: perspectives from the mountains of California. Canadian Journal of Fisheries and Aquatic Sciences 73(11):1691–1701.

Polato, N. R., B. A. Gill, A. A. Shah, M. M. Gray, K. L. Casner, A. Barthelet, P. W. Messer, M. P. Simmons, J. M. Guayasamin, A. C. Encalada, B. C. Kondratieff, A. S. Flecker, S. A. Thomas, C. K. Ghalambor, N. L. Poff, W. C. Funk, and K. R. Zamudio. 2018. Narrow thermal tolerance and low dispersal drive higher speciation in tropical mountains. Proceedings of the National Academy of Sciences 115(49):12471–12476.

Prather, R. M., R. M. Dalton, billy barr, D. T. Blumstein, C. L. Boggs, A. K. Brody, D. W. Inouye, R. E. Irwin, J. G. A. Martin, R. J. Smith, D. H. Van Vuren, C. P. Wells, H. H. Whiteman, B. D. Inouye, and N. Underwood. 2023. Current and lagged climate affects phenology across diverse taxonomic groups. Proceedings of the Royal Society B: Biological Sciences 290(1990):20222181.

Ralston, D. K., B. A. Keafer, M. L. Brosnahan, and D. M. Anderson. 2014. Temperature dependence of an estuarine harmful algal bloom: Resolving interannual variability in bloom dynamics using a degree-day approach. Limnology and Oceanography 59(4):1112–1126.

Råman Vinnå, L., I. Medhaug, M. Schmid, and D. Bouffard. 2021. The vulnerability of lakes to climate change along an altitudinal gradient. Communications Earth & Environment 2(1):35.

Read, E. K., V. P. Patil, S. K. Oliver, A. L. Hetherington, J. A. Brentrup, J. A. Zwart, K. M. Winters, J. R. Corman, E. R. Nodine, R. I. Woolway, H. A. Dugan, A. Jaimes, A. B. Santoso, G. S. Hong, L. A. Winslow, P. C. Hanson, and K. C. Weathers. 2015. The importance of lake-specific characteristics for water quality across the continental United States. Ecological Applications 25(4):943–955.

Read, J. S., X. Jia, J. Willard, A. P. Appling, J. A. Zwart, S. K. Oliver, A. Karpatne, G. J. A. Hansen, P. C. Hanson, W. Watkins, M. Steinbach, and V. Kumar. 2019. Process-Guided Deep Learning Predictions of Lake Water Temperature. Water Resources Research 55(11):9173–9190.

Reid, A. J., A. K. Carlson, I. F. Creed, E. J. Eliason, P. A. Gell, P. T. J. Johnson, K. A. Kidd, T. J. MacCormack, J. D. Olden, S. J. Ormerod, J. P. Smol, W. W. Taylor, K. Tockner, J. C. Vermaire, D. Dudgeon, and S. J. Cooke. 2019. Emerging threats and persistent conservation challenges for freshwater biodiversity. Biological Reviews 94(3):849–873.

Richard, J. C., and A. L. Rypel. 2013. Water Body Type Influences Climate–Growth Relationships of Freshwater Drum. Transactions of the American Fisheries Society 142(5):1308–1320.

Richardson, D. C., M. A. Holgerson, M. J. Farragher, K. K. Hoffman, K. B. S. King, M. B. Alfonso, M. R. Andersen, K. S. Cheruveil, K. A. Coleman, M. J. Farruggia, R. L.

Fernandez, K. L. Hondula, G. A. López Moreira Mazacotte, K. Paul, B. L. Peierls, J. S. Rabaey, S. Sadro, M. L. Sánchez, R. L. Smyth, and J. N. Sweetman. 2022. A functional definition to distinguish ponds from lakes and wetlands. Scientific Reports 12(1):10472.

Richman, S. K., J. M. Levine, L. Stefan, and C. A. Johnson. 2020. Asynchronous range shifts drive alpine plant–pollinator interactions and reduce plant fitness. Global Change Biology 26(5):3052–3064.

Rolla, M., G. Biffoni, S. Brighenti, R. Iacobuzio, K. Liautaud, C. Pasquaretta, and R. Tiberti. 2018. Predation by introduced fish can magnify the terrestrial arthropod subsidies in mountain lakes. Canadian Journal of Fisheries and Aquatic Sciences 75(9):1453–1464.

Rypel, A. 2015. Meta-Analysis of Growth for Five North American Catfishes: Effects of Climate, Hydrologic Habitat, and Latitudinal Countergradients.

Rypel, A. L. 2012a. Meta-analysis of growth rates for a circumpolar fish, the northern pike (Esox lucius), with emphasis on effects of continent, climate and latitude. Ecology of Freshwater Fish 21(4):521–532.

Rypel, A. L. 2012b. Concordant estimates of countergradient growth variation in striped bass (Morone saxatilis) using comparative life-history data. Canadian Journal of Fisheries and Aquatic Sciences 69(8):1261–1265.

Rypel, A. L. 2014a. Do invasive freshwater fish species grow better when they are invasive? Oikos 123(3):279–289.

Rypel, A. L. 2014b. The Cold-Water Connection: Bergmann's Rule in North American Freshwater Fishes. The American Naturalist 183(1):147–156.

Rypel, A. L. 2023. Ecosystem size filters life-history strategies to shape community assembly in lakes. Journal of Animal Ecology 92(6):1161–1175.

Rypel, A. L. In Revision. Speed of change in freshwater fish populations. Freshwater Biology.

Rypel, A. L., and S. R. David. 2017. Pattern and scale in latitude–production relationships for freshwater fishes. Ecosphere 8(1):e01660.

Rypel, A. L., T. D. Simonson, D. L. Oele, J. D. Griffin, T. P. Parks, D. Seibel, C. M. Roberts, S. Toshner, L. S. Tate, and J. Lyons. 2019a. Flexible classification of Wisconsin lakes for improved fisheries conservation and management. Fisheries 44(5):225–238.

Rypel, A. L., T. D. Simonson, D. L. Oele, J. D. T. Griffin, T. P. Parks, D. Seibel, C. M. Roberts, S. Toshner, L. S. Tate, and J. Lyons. 2019b. Flexible Classification of Wisconsin Lakes for Improved Fisheries Conservation and Management. Fisheries 44(5):225–238.

Rypel, A., and J. Magnuson. 2019. Rehabilitation and a safe operating space for freshwater fisheries. Page *in* D. Hamilton, K. Collier, C. Howard-Williams, and J. Quinn, editors. Lake Restoration Handbook. Springer, Switzerland.

Sabás, I., A. Miró, J. Piera, J. Catalan, L. Camarero, T. Buchaca, and M. Ventura. 2021. Factors of surface thermal variation in high-mountain lakes of the Pyrenees. PLOS ONE 16(8):e0254702.

Sadro, S., J. M. Melack, J. O. Sickman, and K. Skeen. 2019. Climate warming response of mountain lakes affected by variations in snow. Limnology and Oceanography Letters 4(1):9–17.

Schai-Braun, S. C., H. Jenny, T. Ruf, and K. Hackländer. 2021. Temperature increase and frost decrease driving upslope elevational range shifts in Alpine grouse and hares. Global Change Biology 27(24):6602–6614.

Scheffer, M. 1990. Multiplicity of stable states in freshwater systems. Pages 475–486 *in* R. D. Gulati, E. H. R. R. Lammens, M.-L. Meijer, and E. van Donk, editors. Biomanipulation Tool for Water Management. Springer Netherlands, Dordrecht.

Scheffer, M., and S. R. Carpenter. 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. Trends in Ecology & Evolution 18(12):648–656.

Schupp, D. H. 1992. An ecological classification of Minnesota lakes with associated fish communities. Minnesota Department of Natural Resources, Section of Fisheries, 417.

Seamster, A. P. 1950. Developmental Studies Concerning the Eggs of Ascaris lumbricoides var. suum. The American Midland Naturalist 43(2):450–470.

Seuffert, M. E., L. Saveanu, and P. R. Martín. 2012. Threshold Temperatures and Degree-Day Estimates for Embryonic Development of the Invasive Apple Snail Pomacea canaliculata (Caenogastropoda: Ampullariidae). Malacologia 55(2):209–217.

Shah, A. A., B. A. Gill, A. C. Encalada, A. S. Flecker, W. C. Funk, J. M. Guayasamin, B. C. Kondratieff, N. L. Poff, S. A. Thomas, K. R. Zamudio, and C. K. Ghalambor. 2017. Climate variability predicts thermal limits of aquatic insects across elevation and latitude. Functional Ecology 31(11):2118–2127.

Shah, R. D. T., D. Narayan Shah, and S. Domisch. 2012. Range shifts of a relict Himalayan dragonfly in the Hindu Kush Himalayan region under climate change scenarios. International Journal of Odonatology 15(3):209–222.

Shepard, I. D., S. A. Wissinger, and H. S. Greig. 2021. Elevation alters outcome of competition between resident and range-shifting species. Global Change Biology 27(2):270–281.

Spurgeon, J. J., M. A. Pegg, K. L. Pope, and L. Xie. 2020. Ecosystem-specific growth responses to climate pattern by a temperate freshwater fish. Ecological Indicators 112:106130.

Stachelek, J. 2019. Tools for working with the National Hydrography Dataset. https://cran.r-project.org/package=nhdR.

Sunday, J., J. M. Bennett, P. Calosi, S. Clusella-Trullas, S. Gravel, A. L. Hargreaves, F. P. Leiva, W. C. E. P. Verberk, M. Á. Olalla-Tárraga, and I. Morales-Castilla. 2019. Thermal tolerance patterns across latitude and elevation. Philosophical Transactions of the Royal Society B: Biological Sciences 374(1778):20190036.

Suzuki, H., M. Takenaka, and K. Tojo. 2024. Evolutionary history of a cold-adapted limnephilid caddisfly: Effects of climate change and topography on genetic structure. Molecular Phylogenetics and Evolution 191:107967.

Tassone, S. J., and M. L. Pace. 2024. Increased Frequency of Sediment Heatwaves in a Virginia Seagrass Meadow. Estuaries and Coasts 47(3):656–669.

Thompson, R., C. Kamenik, and R. Schmidt. 2005. Ultra-sensitive Alpine lakes and climate change. Journal of Limnology 64(2):139.

Tickner, D., J. J. Opperman, R. Abell, M. Acreman, A. H. Arthington, S. E. Bunn, S. J. Cooke, J. Dalton, W. Darwall, G. Edwards, I. Harrison, K. Hughes, T. Jones, D. Leclère, A. J. Lynch, P. Leonard, M. E. McClain, D. Muruven, J. D. Olden, S. J. Ormerod, J. Robinson, R. E. Tharme, M. Thieme, K. Tockner, M. Wright, and L. Young. 2020. Bending the Curve of Global Freshwater Biodiversity Loss: An Emergency Recovery Plan. BioScience 70(4):330–342.

Till, A., A. L. Rypel, A. Bray, and S. B. Fey. 2019. Fish die-offs are concurrent with thermal extremes in north temperate lakes. Nature Climate Change 9(8):637–641.

Tulloch, V. J., A. I. Tulloch, P. Visconti, B. S. Halpern, J. E. Watson, M. C. Evans, N. A. Auerbach, M. Barnes, M. Beger, I. Chadès, S. Giakoumi, E. McDonald-Madden, N. J.

Murray, J. Ringma, and H. P. Possingham. 2015. Why do we map threats? Linking threat mapping with actions to make better conservation decisions. Frontiers in Ecology and the Environment 13(2):91–99.

Uphoff, C. S., C. W. Schoenebeck, W. W. Hoback, K. D. Koupal, and K. L. Pope. 2013. Degree-day accumulation influences annual variability in growth of age-0 walleye. Fisheries Research 147:394–398.

USGS. 2022. National Hydrography Dataset. Technical Report. United States Geological Survey. https://www.usgs.gov/national-hydrography.

Van Tatenhove, A., E. Filiberti, T. S. Sillett, N. Rodenhouse, and M. Hallworth. 2019. Climate-Related Distribution Shifts of Migratory Songbirds and Sciurids in the White Mountain National Forest. Forests 10(2):84.

Vanderkelen, I., N. P. M. van Lipzig, D. M. Lawrence, B. Droppers, M. Golub, S. N. Gosling, A. B. G. Janssen, R. Marcé, H. M. Schmied, M. Perroud, D. Pierson, Y. Pokhrel, Y. Satoh, J. Schewe, S. I. Seneviratne, V. M. Stepanenko, Z. Tan, R. I. Woolway, and W. Thiery. 2020. Global Heat Uptake by Inland Waters. Geophysical Research Letters 47(12):e2020GL087867.

Venables, W. N., and B. D. Ripley. 2002. Modern Applied Statistics with S, 4th edition. Springer, New York. ISBN 0-387-95457-0, https://www.stats.ox.ac.uk/pub/MASS4/.

Venturelli, P. A., N. P. Lester, T. R. Marshall, and B. J. Shuter. 2010. Consistent patterns of maturity and density-dependent growth among populations of walleye (Sander vitreus): application of the growing degree-day metric. Canadian Journal of Fisheries and Aquatic Sciences 67(7):1057–1067.

Vitasse, Y., S. Ursenbacher, G. Klein, T. Bohnenstengel, Y. Chittaro, A. Delestrade, C. Monnerat, M. Rebetez, C. Rixen, N. Strebel, B. R. Schmidt, S. Wipf, T. Wohlgemuth, N. G. Yoccoz, and J. Lenoir. 2021. Phenological and elevational shifts of plants, animals and fungi under climate change in the European Alps. Biological Reviews 96(5):1816–1835.

Viterbi, R., C. Cerrato, R. Bionda, and A. Provenzale. 2020. Effects of Temperature Rise on Multi-Taxa Distributions in Mountain Ecosystems. Diversity 12(6):210.

Viviroli, D., D. R. Archer, W. Buytaert, H. J. Fowler, G. B. Greenwood, A. F. Hamlet, Y. Huang, G. Koboltschnig, M. I. Litaor, J. I. López-Moreno, S. Lorentz, B. Schädler, H. Schreier, K. Schwaiger, M. Vuille, and R. Woods. 2011. Climate change and mountain water resources: overview and recommendations for research, management and policy. Hydrology and Earth System Sciences 15(2):471–504.

Watanabe, T., M. Suzuki, Y. Komoto, K. Shirai, and A. Yamazaki. 2021. Daily and annual shell growth in a long-lived freshwater bivalve as a proxy for winter snowpack. Palaeogeography, Palaeoclimatology, Palaeoecology 569:110346.

Wehrly, K. E., J. E. Breck, L. Wang, and L. Szabo-Kraft. 2012. A landscape-based classification of fish assemblages in sampled and unsampled lakes. Transactions of the American Fisheries Society 141(2):414–425.

Willard, J. D., J. S. Read, A. P. Appling, S. K. Oliver, X. Jia, and V. Kumar. 2021. Predicting Water Temperature Dynamics of Unmonitored Lakes With Meta-Transfer Learning. Water Resources Research 57(7):e2021WR029579.

Willis, A. D., R. A. Peek, and A. L. Rypel. 2021. Classifying California’s stream thermal regimes for cold-water conservation. PLOS ONE 16(8):e0256286.

Wilsie, C. P., and R. H. Shaw. 1954. Crop Adaptation and Climate. Pages 199–252 *in* A. G. Norman, editor. Advances in Agronomy. Academic Press.

Woodward, G., D. M. Perkins, and L. E. Brown. 2010. Climate change and freshwater ecosystems: impacts across multiple levels of organization. Philosophical Transactions of the Royal Society B: Biological Sciences 365(1549):2093–2106.

Woolway, R. I. 2023. The pace of shifting seasons in lakes. Nature Communications 14(1):2101.

Woolway, R. I., and S. C. Maberly. 2020. Climate velocity in inland standing waters. Nature Climate Change 10(12):1124–1129.

Woolway, R. I., and C. J. Merchant. 2019. Worldwide alteration of lake mixing regimes in response to climate change. Nature Geoscience 12(4):271–276.

Woolway, R. I., S. Sharma, G. A. Weyhenmeyer, A. Debolskiy, M. Golub, D. Mercado-Bettín, M. Perroud, V. Stepanenko, Z. Tan, L. Grant, R. Ladwig, J. Mesman, T. N. Moore, T. Shatwell, I. Vanderkelen, J. A. Austin, C. L. DeGasperi, M. Dokulil, S. La Fuente, E. B. Mackay, S. G. Schladow, S. Watanabe, R. Marcé, D. C. Pierson, W. Thiery, and E. Jennings. 2021. Phenological shifts in lake stratification under climate change. Nature Communications 12(1):2318.

Wu, F., X. Deng, Q. O. Jiang, J. Zhan, and D. Liu. 2012. Analysis of lake vulnerability in the middle-lower Yangtze River catchment using C4.5 decision tree algorithms. Journal of Food, Agriculture & Environment 10(2):1245–1247.

Xu, T., B. Weng, D. Yan, K. Wang, X. Li, W. Bi, M. Li, X. Cheng, and Y. Liu. 2019. Wetlands of International Importance: Status, Threats, and Future Protection. International Journal of Environmental Research and Public Health 16(10):1818.

Yvon-Durocher, G., J. M. Montoya, M. Trimmer, and G. Woodward. 2011. Warming alters the size spectrum and shifts the distribution of biomass in freshwater ecosystems. Global Change Biology 17(4):1681–1694.

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Figures & Tables

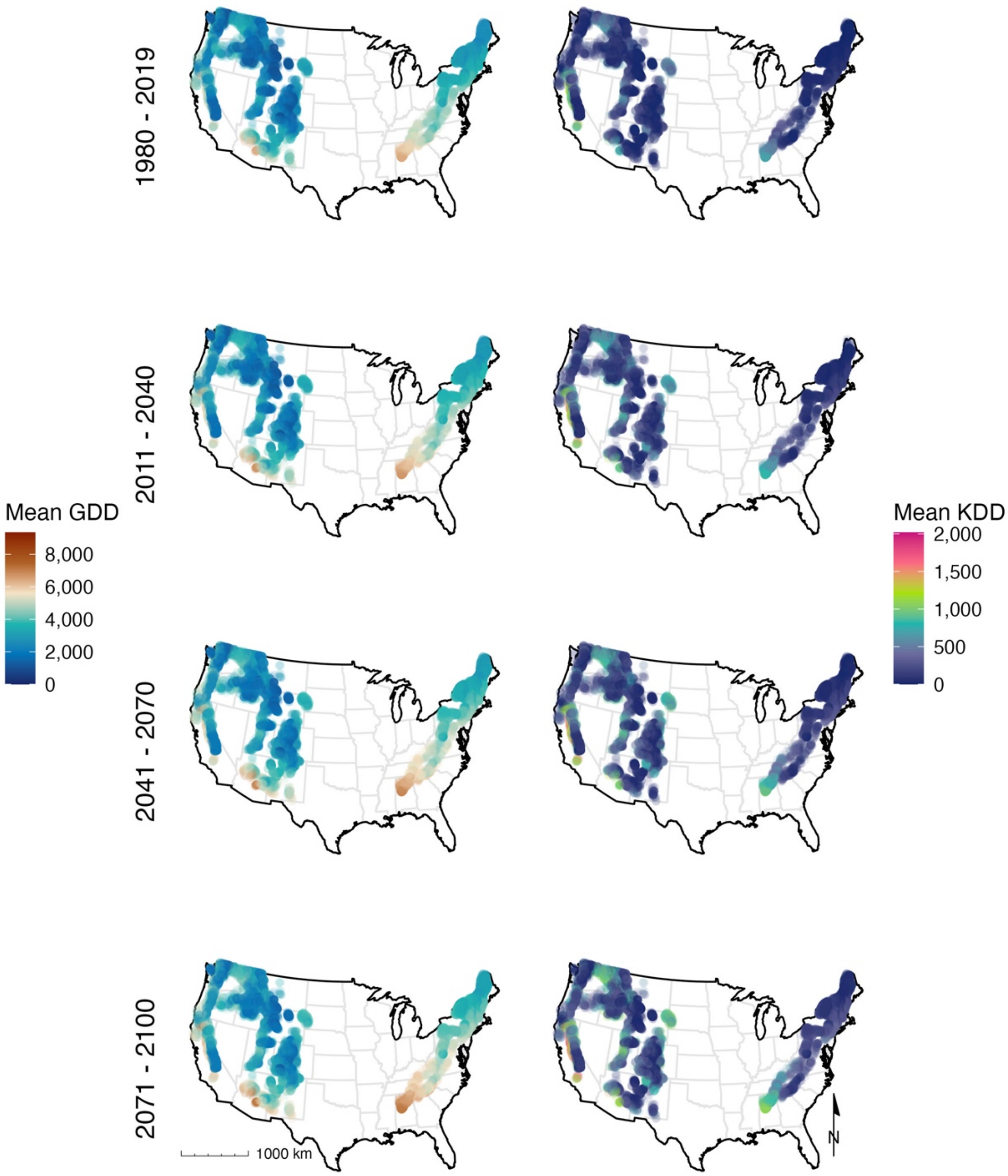

Figure 1

Mean Growing Degree Days (GDD; left panel) and Killing Degree Days (KDD; right panel) across mountain lake landscapes in the contiguous USA for the time periods: 1980–2019, 2011–2040, 2041–2070, 2071–2100.

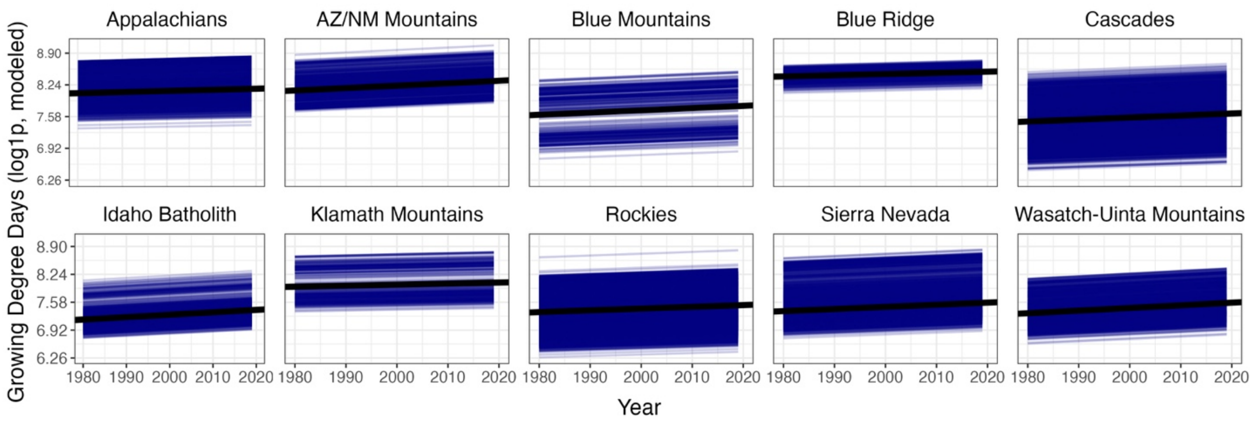

Figure 2

Long-term trends in GDD for mountain lake landscapes in 10 mountain ranges across the USA as assayed using random slope and random intercept linear mixed effect models. Dark parent line denotes overall trend for each region.

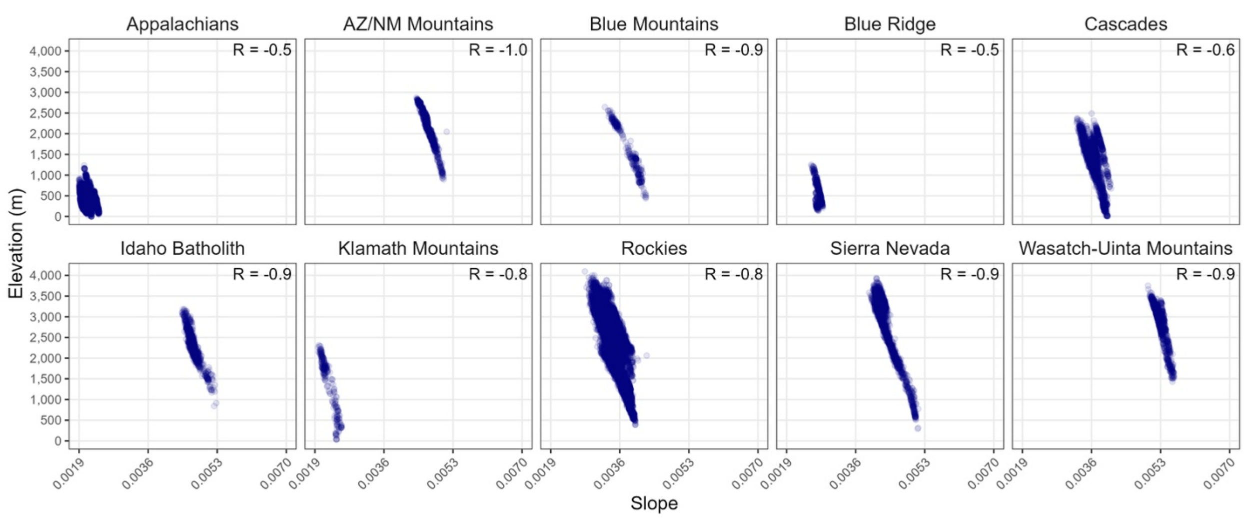

Figure 3

Velocity of climate change (assayed as random slopes extracted from the random slope and random intercept linear mixed effect model) plotted against elevation of mountain lakes. Pearson correlation coefficient (R) is shown in upper right of each plot.

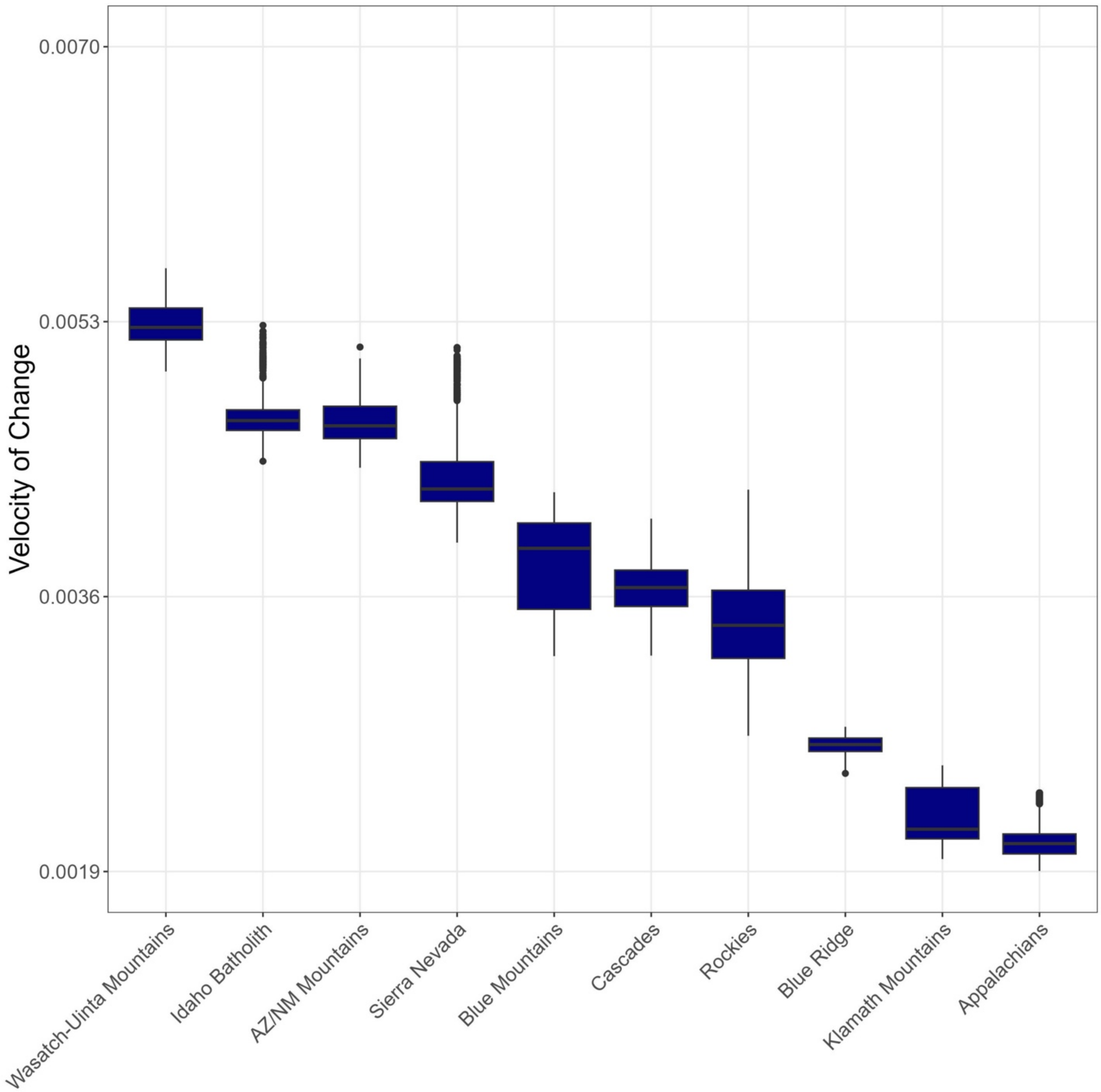

Figure 4

Box plots showing the range of observed velocities of change (random effect slopes) in each focal mountain range. Each box represents the median value and interquartile range, and error bars denote the 95% confidence interval.

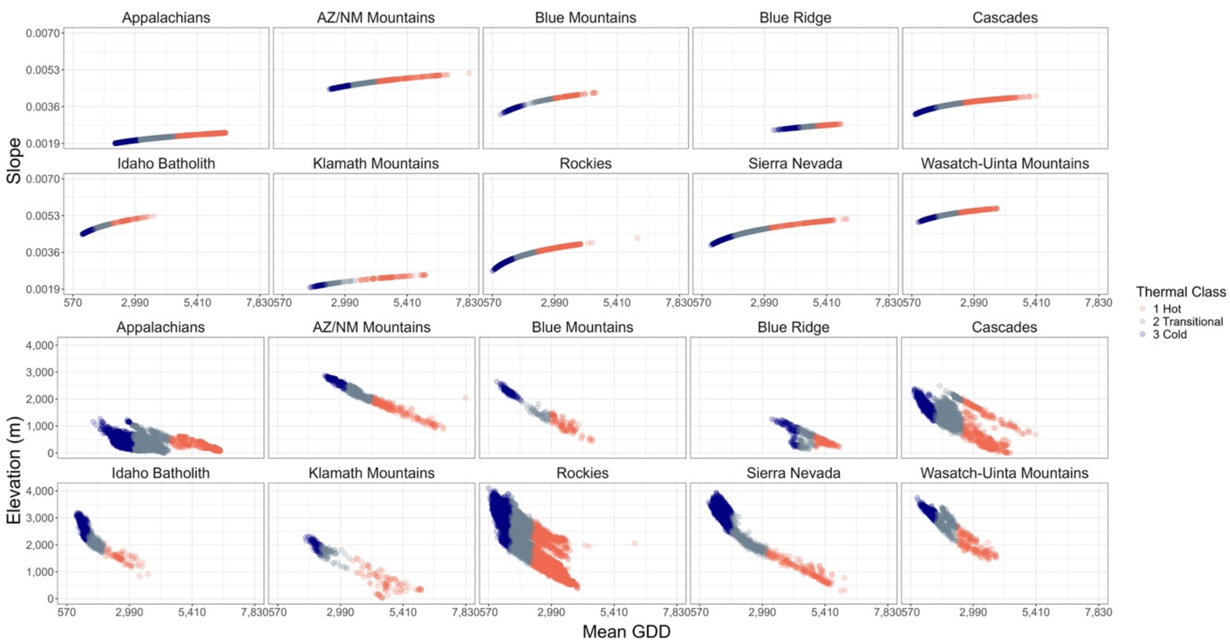

Figure 5

Relationship of velocity of change (random effect slopes) and elevation as a function of mean GDD for each lake in 10 major mountain ranges in the USA. In each plot, each unique lake landscape is identified by its membership in each of the three climate vulnerability classes.

Table 1

Summary of membership totals (historical and future) in each of three climate vulnerability classes for major mountain ranges in the contiguous United States, including percentage of lakes (non-bold) and percent change (bold) from the historic time period.

Region	Time Period (1980–)	Percentage of Lakes & Percent Change from Historic Baseline		
		Cold	Transitional	Hot
All	2019	42	39	19
	2040	25 (**-40**)	52 (**34**)	22 (**21**)
	2070	16 (**-62**)	57 (**46**)	26 (**43**)
	2100	8 (**-82**)	59 (**51**)	33 (**80**)
1. Appalachians	2019	45	44	10
	2040	26 **(-42)**	63 **(42)**	11 **(4)**
	2070	16 **(-66)**	72 **(62)**	12 **(21)**
	2100	5 **(-89)**	76 **(70)**	19 **(86)**
2. Arizona–New Mexico Mountains	2019	25	45	30
	2040	16 **(-36)**	47 **(4)**	37 **(24)**
	2070	7 **(-72)**	51 **(12)**	42 **(42)**
	2100	1 **(-98)**	45 **(-1)**	55 **(85)**
3. Blue Mountains	2019	40	19	41
	2040	38 **(-6)**	12 **(-34)**	50 **(21)**
	2070	36 **(-11)**	12 **(-34)**	52 **(26)**
	2100	23 **(-44)**	21 **(13)**	56 **(37)**
4. Blue Ridge	2019	23	44	33

	2040	8 **(-65)**	38 **(-14)**	54 **(64)**
	2070	4 **(-82)**	31 **(-31)**	65 **(99)**
	2100	1 **(-94)**	16 **(-64)**	83 **(153)**
5. Cascades	2019	28	48	24
	2040	17 **(-40)**	55 **(14)**	28 **(17)**
	2070	13 **(-55)**	56 **(15)**	32 **(35)**
	2100	7 **(-75)**	51 **(6)**	42 **(77)**
6. Idaho Batholith	2019	49	43	8
	2040	11 **(-78)**	80 **(84)**	10 **(29)**
	2070	4 **(-92)**	81 **(88)**	15 **(95)**
	2100	1 **(-99)**	75 **(74)**	24 **(221)**
7. Klamath Mountains	2019	30	33	38
	2040	9 **(-71)**	52 **(60)**	39 **(4)**
	2070	3 **(-90)**	57 **(75)**	40 **(7)**
	2100	1 **(-97)**	57 **(74)**	42 **(13)**
8. Rockies	2019	38	35	27
	2040	22 **(-41)**	44 **(26)**	33 **(25)**
	2070	15 **(-62)**	45 **(29)**	40 **(50)**
	2100	7 **(-81)**	47 **(32)**	46 **(73)**
9. Sierra Nevada	2019	67	24	9
	2040	54 **(-20)**	36 **(50)**	11 **(21)**
	2070	42 **(-38)**	47 **(96)**	12 **(32)**
	2100	26 **(-62)**	61 **(155)**	14 **(57)**
10. Wasatch-Uinta Mountains	2019	47	33	20
	2040	23 **(-51)**	50 **(52)**	27 **(37)**
	2070	14 **(-70)**	53 **(61)**	32 **(66)**
	2100	6 **(-87)**	55 **(68)**	38 **(96)**

Supplement

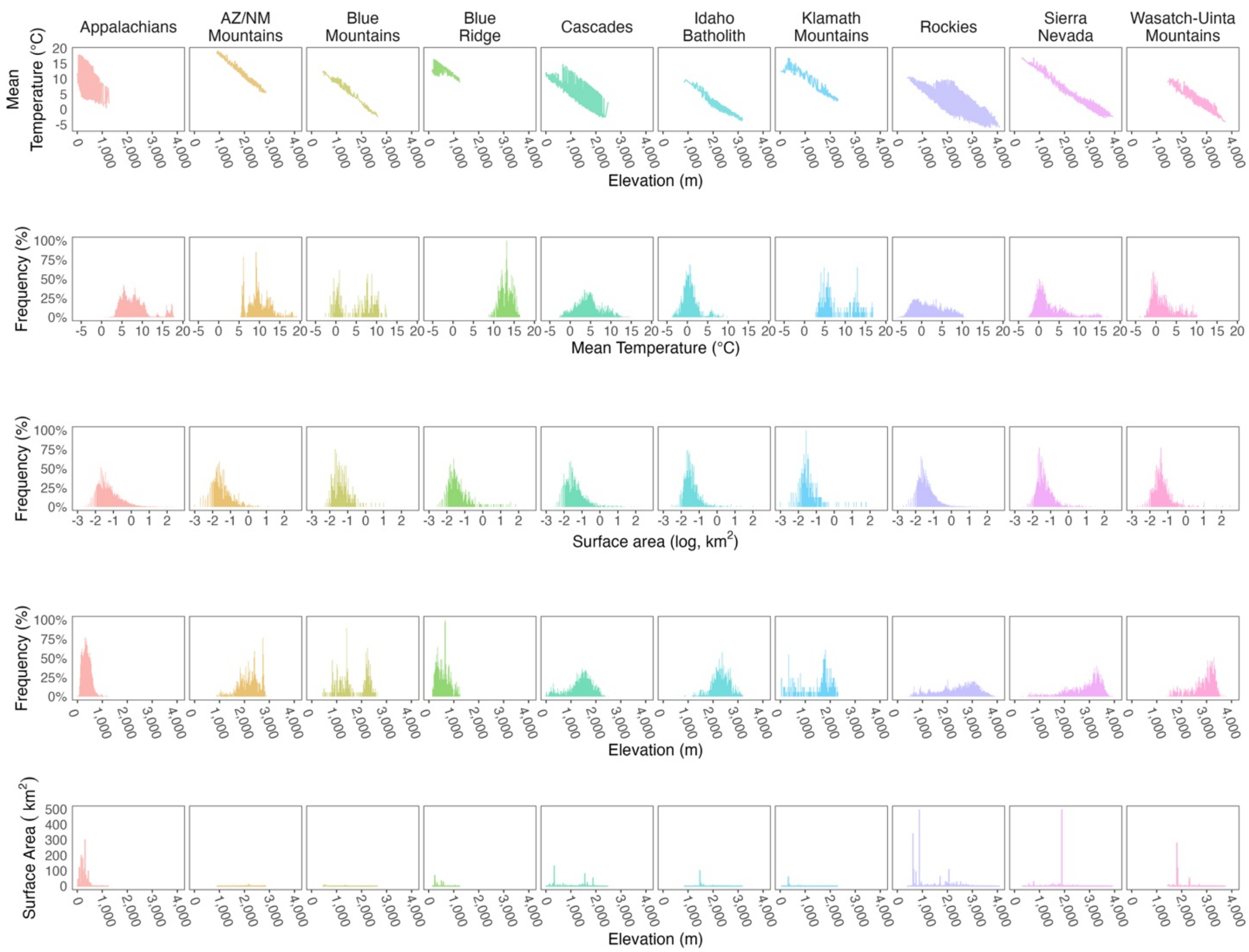

Figure S1

Frequency histograms for temperature (°C), lake surface area (log, km^2), and elevation (m) for lakes in 10 USA mountain ranges. Surface area as a function of elevation is shown to provide context and highlight lake diversity across ranges. Data were obtained from the National Hydrography Database (NHD) and CHELSA Database. Plotted temperature represents the average temperature 1980–2019 for a lake point in the NHD.

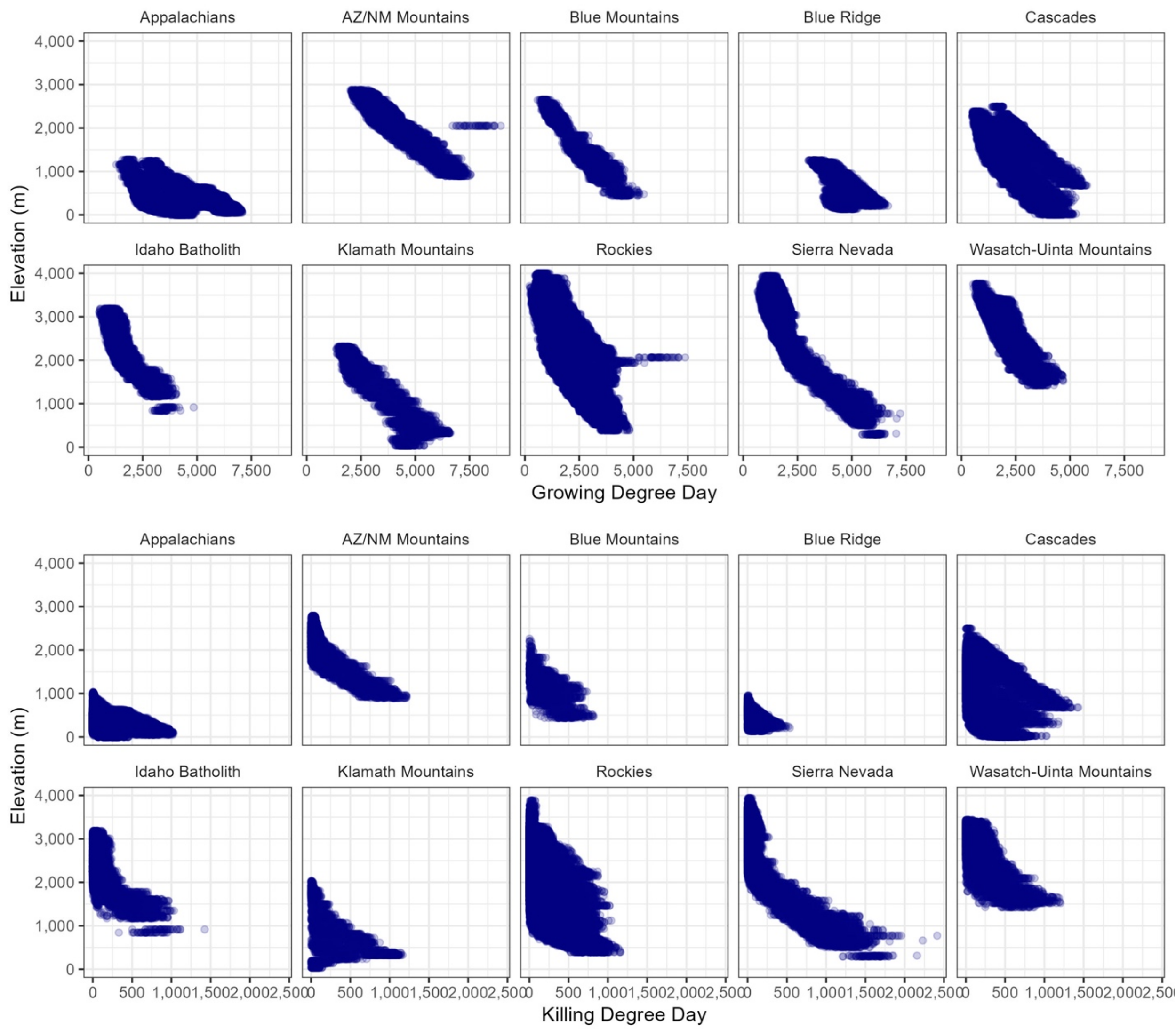

Figure S2

Historical sum of growing degree day and killing degree day as a function of elevation. Each point represents a unique *Lake–Year* combination.

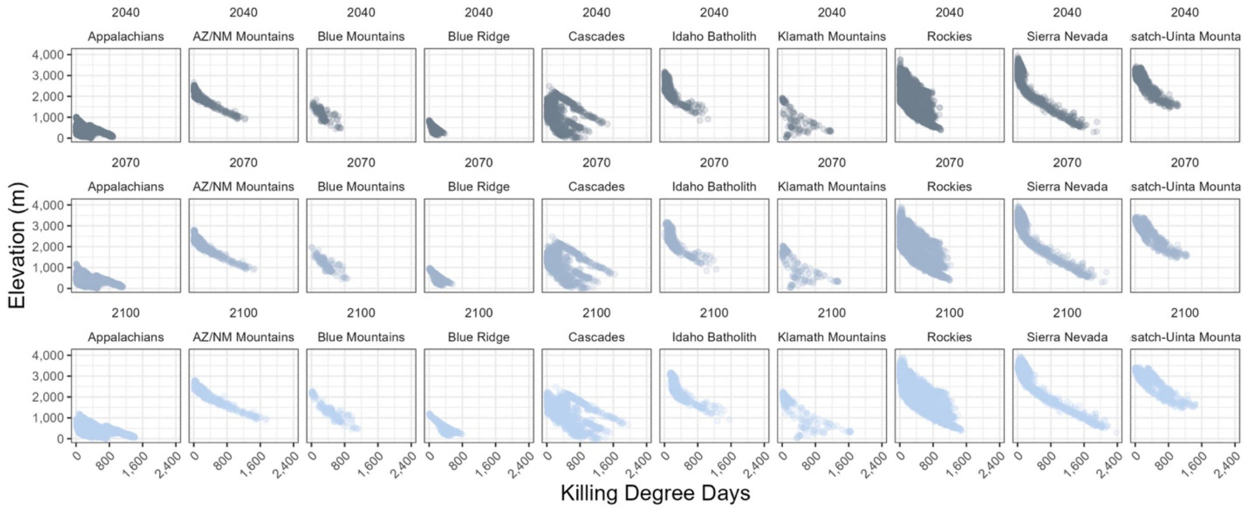

Figure S3

Projected killing degree days as a function of elevation. Each point represents a unique *Lake–Year* combination.

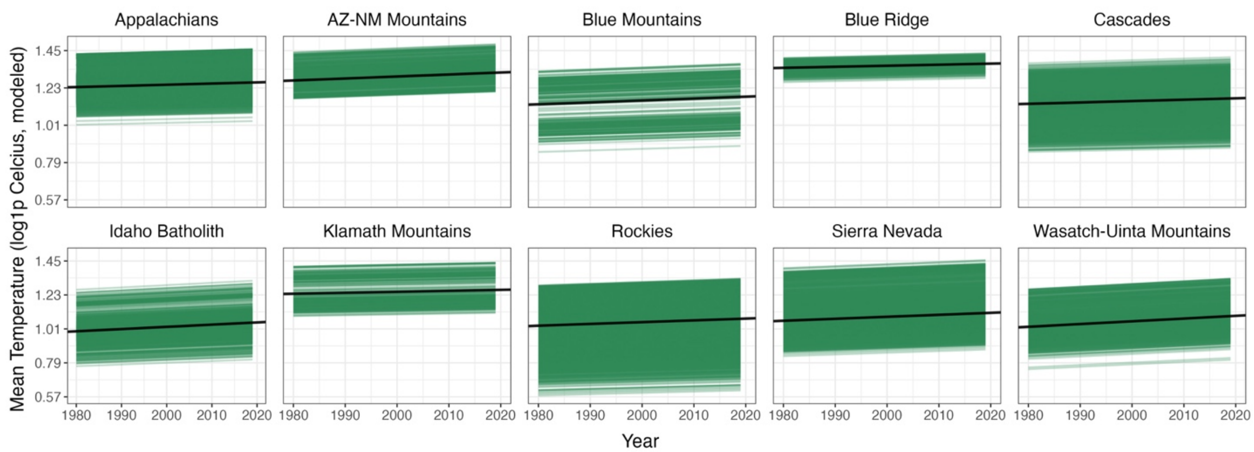

Figure S4

Long-term trends in temperature for mountain lake landscapes in 10 mountain ranges across the USA as assayed using random slope and random intercept linear mixed effect models. Dark parent line denotes overall trend for each region.

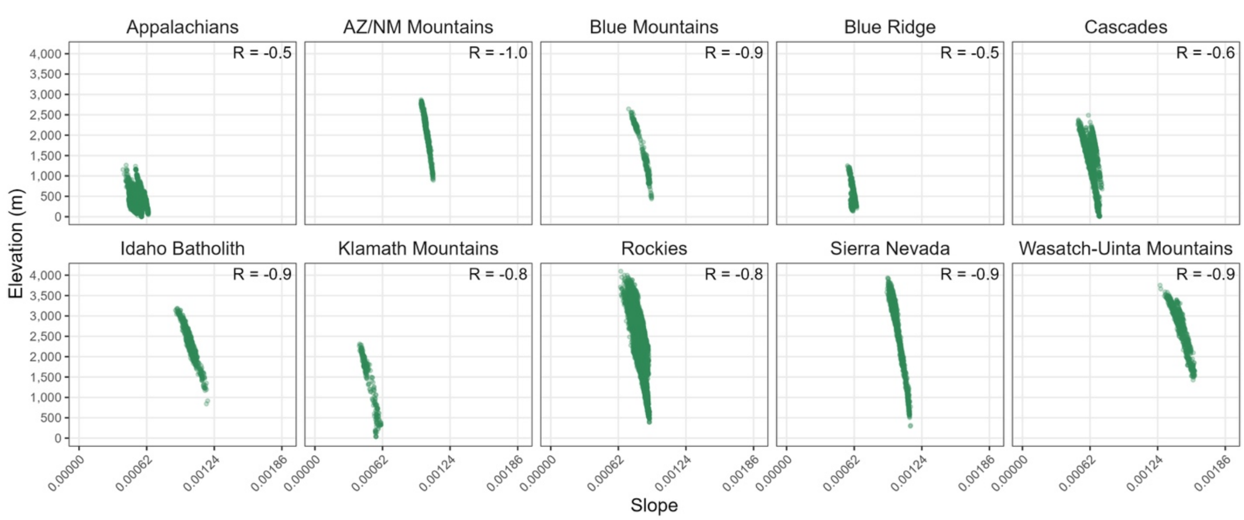

Figure S5

Velocity of temperature change (assayed as random slopes extracted from the random slope and random intercept linear mixed effect model) plotted against elevation of mountain lakes. Pearson correlation coefficient (R) is shown in upper right of each plot.

Figure S6

Boxplots of mean GDD, mean KDD, elevation, and velocity of change (random effect slopes) in each lake landscape and climate vulnerability category. In each plot, boxes represent the median and interquartile range.

Table S1

Descriptive statistics of statistical moments for the distributions of surface area (km^2) and elevation (m) for each studied mountain range.

Mountain Range	Lake Abundance (n)	Surface Area (km^2)			Elevation (m)		
		Skew	Kurtosis	Mean	Skew	Kurtosis	Mean
1. Appalachians	10,467	33.3	1,376.3	0.4	0.7	4.0	369
2. Arizona–New Mexico Mountains	1,033	17.9	418.3	0.1	-0.6	3.1	2,189
3. Blue Mountains	284	10.9	134.3	0.1	0.0	1.6	1,614
4. Blue Ridge	464	11.2	150.1	0.6	0.5	2.5	581
5. Cascades	2,165	26.9	844.4	0.3	-0.7	3.0	1,361
6. Idaho Batholith	1,035	29.4	908.9	0.2	-0.4	3.5	2,313
7. Klamath Mountains	245	10.7	128.9	0.6	-0.6	1.9	1,378
8. Rockies	9,661	62.1	4282.3	0.3	-0.5	2.3	2,375
9. Sierra Nevada	2,358	47.8	2305.4	0.4	-1.1	3.8	2,788
10. Wasatch-Uinta	988	25.1	681.2	0.6	-1.0	3.1	2,847

Table S2

Summary statistics for linear mixed-effect regression models (*Temperature ~ Year (Year | LakeID)*) from which velocity of climate change metrics were extracted.

Mountain Range	Pseudo R^2	Parent Intercept	Parent Slope	Model Slope (Year Effect) df	t-value	p-value
	Growing Degree Days (1980–2019)					
1. Appalachians	0.97	3.48	0.0023	1,142	370	<0.0001
2. Arizona–New Mexico Mountain	0.96	-1.86	0.0050	37,799	226	<0.0001
3. Blue Mountains	0.97	-1.53	0.0046	2,120	70	<0.0001
4. Blue Ridge	0.89	3.56	0.0025	8,434	93	<0.0001
5. Cascades	0.95	-0.79	0.0042	10,022	150	<0.0001
6. Idaho Batholith	0.86	-4.21	0.0057	39,612	132	<0.0001
7. Klamath Mountains	0.97	3.07	0.0025	1,858	39	<0.0001
8. Rockies	0.95	-0.82	0.0041	371,846	297	<0.0001
9. Sierra Nevada	0.96	-2.62	0.0050	6,879	201	<0.0001
10. Wasatch-Uinta Mountains	0.94	-5.14	0.0063	18,566	159	<0.0001
	Temperature (1980–2019)					
1. Appalachians	0.96	-0.14	0.0007	135,980	313	<0.0001
2. Arizona–New Mexico Mountain	0.96	-1.06	0.0012	94,82	188	<0.0001
3. Blue Mountains	0.97	-1.09	0.0011	10,920	58	<0.0001
4. Blue Ridge	0.89	0.12	0.0006	9,618	93	<0.0001

5. Cascades	0.96	-0.47	0.0008	77,688	132	<0.0001
6. Idaho Batholith	0.90	-1.85	0.0014	6,367	116	<0.0001
7. Klamath Mountains	0.97	-0.01	0.0006	1,882	43	<0.0001
8. Rockies	0.96	-1.25	0.0012	44,117	274	<0.0001
9. Sierra Nevada	0.96	-1.49	0.0013	91,413	182	<0.0001
10. Wasatch-Uinta Mountains	0.95	-2.50	0.0018	13,220	157	<0.0001

Table S3

Summary statistics of Discriminant Function Analyses (DFAs) predicting lake landscape membership into each of three climate vulnerability classes.

	DFA models using 80% as training and 20% as testing dataset		
Mountain Range	Accuracy (%)	p-value	Coefficients of Linear Discriminants
1. Appalachians	100	<0.0001	12.30
2. Arizona–New Mexico Mountains	95	<0.0001	10.90
3. Blue Mountains	96	<0.0001	8.35
4. Blue Ridge	96	<0.0001	21.94
5. Cascades	96	<0.0001	6.44
6. Idaho Batholith	99	<0.0001	10.87
7. Klamath Mountains	94	<0.0001	9.25
8. Rockies	99	<0.0001	6.81
9. Sierra Nevada	97	<0.0001	7.44
10. Wasatch-Uinta Mountains	98	<0.0001	8.30