

Ecological condition of mountain lakes in the conterminous United States and vulnerability to human development

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ABSTRACT

Mountain lakes provide cultural, aesthetic, and recreational services across the globe. Despite their recognized importance, there is no consistent definition of a mountain lake, which hampers describing them individually as well as in aggregate. Additionally, it makes it difficult to study and manage this unique population. We develop a rules-based approach for classifying mountain lakes according to the topography of the area draining directly to the lake. We apply the approach to the data from the United States National Lakes Assessment, for which the population is defined as lakes that are at least 1 ha in surface area and at least 1 m deep in the conterminous US (CONUS). Leveraging this national assessment allows for evaluating the condition of mountain lakes relative to all lakes in the CONUS. There are an estimated 12,353 (95 % C.I. 10,529–14,177) mountain lakes that account for 6.4 % of the lake population in the CONUS. Mountain lakes are in better condition than non-mountain lakes for 11 of 12 physical, chemical, and biological indicators (acid neutralizing capacity was the one exception). Approximately 25 % of mountain lakes are classified as eutrophic or hypereutrophic, and nearly 50 % are in fair or poor condition with respect to riparian vegetation and lakeshore disturbance. Mountain lake watersheds have lower proportions of developed land cover ($\text{mean} \pm 95\% \text{ CI}: 0.8 \pm 0.1\%$) compared to non-mountain lakes ($6.7 \pm 0.3\%$); however, developed land cover is more concentrated closer to the lakeshore for mountain lakes compared to non-mountain lakes. Coupled with characteristics such as high runoff, low hydraulic conductivity, and shallow bedrock depths, mountain lakes may be more susceptible to the adverse effects of human development and climate change compared to non-mountain lakes. These findings underscore the need for targeted monitoring, conservation, and management strategies to protect these valuable and sensitive lake environments.

1. Introduction

Mountain lakes are widely recognized for their scenic beauty and clear waters (Schirpke et al., 2021). In the ecological literature, mountain lakes are typically characterized by high elevation, cool water temperatures, oligotrophic conditions with high water clarity and low nutrients, seasonal ice cover, and low anthropogenic influence (Catalán

et al., 2006; Moser et al., 2019). As freshwater resources upstream of many human communities, mountains lakes are commonly referred to as water towers of the planet (Messerli et al., 2004). In addition, mountain lakes support sensitive and unique biota (Palomo, 2017) have high cultural significance, provide hazard mitigation, and also serve as centers for recreational activity (Ebner et al., 2022a). Since mountain lakes are widely acknowledged as highly valued ecosystems and

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components of larger ecosystems, studies of their status and condition as a population are needed (Catalán et al., 2009b; Moser et al., 2019).

Due to their relative remoteness and potential sensitivity, mountain lakes may serve as sentinels to certain anthropogenic stressors including changing climatic conditions and atmospheric deposition (Catalán et al., 2006; Moser et al., 2019). Rising temperatures and reduced ice cover may lead to a variety of changes in processes such as freeze-thaw, albedo, as well as stratification and mixing (Rangwala and Miller, 2012). Atmospheric deposition and watershed runoff may also contribute new chemical pollutants (Machate et al., 2023) such as microplastics (Pastorino et al., 2022). Climate change may result in mountain lakes experiencing more wildfires and drought, lower land stability and increased floods (Palomo, 2017; Stoffel and Huggel, 2012), as well as changes in species composition and shifting treelines with consequences for lake dissolved organic matter (Catalán et al., 2024). In-lake changes include increases in phytoplankton biomass, alterations in phenological patterns, and shifts in composition that potentially favor cyanobacterial blooms that can impact food webs (Jansen et al., 2024; Woolway et al., 2020). Finally, many mountain lakes are directly impacted by human communities, including activities such as development for recreation, residential use, agriculture, and water supply which can impact the lake (Ebner et al., 2022a; Ebner et al., 2022b; Palomo, 2017; Pastorino et al., 2024; Schirpke and Ebner, 2022).

While the importance and vulnerability of mountain lake ecosystems are well-recognized (Moser et al., 2019), there is currently no comprehensive assessment of the condition of mountain lakes as a distinct population. In fact, there is no rigorous and repeatable definition for “mountain lakes” making such a comprehensive assessment challenging. Historically, alpine lakes have received much attention and concern given their relative remoteness and sensitivity to climate change (Catalán et al., 2006). Alpine lakes are generally considered to occur in high elevation mountainous areas, are at or above the treeline, and are influenced by extended periods of snow or ice cover (Catalán et al., 2009a; Thomasson, 1956). In the conterminous US (CONUS), these definitions would exclude all lakes in the eastern half of the country as well as many lakes occurring in areas referred to as mountains across the CONUS that are of high cultural, aesthetic, and recreational value. For example, Lake Tahoe is a commonly cited as an alpine lake (Richards et al., 1991) although the lake setting does not meet most common definitions of alpine lakes. Despite this, Lake Tahoe and many other mountain lakes are undoubtably important systems that warrant study.

For a mountain lake classification, a simple, fixed elevation cutoff does not suffice since mountain regions occur at many different elevations. A cutoff would likely exclude most or all lower lying mountain regions, while being overly inclusive of non-mountain regions such as plateaus (Moser et al., 2019). For example, in the eastern US, there are the Appalachian Mountains, Smoky Mountains, Green Mountains, Adirondack Mountains, Ozark Mountains, Catskill Mountains, among others; yet these mountain ranges rarely are included in discussions of mountain lakes due to their relatively low elevation compared to mountain ranges of the western US (Immerzeel et al., 2020; Moser et al., 2019). A classification system that relies on data aside from elevation will be required to be inclusive of these eastern mountain ranges. Classification systems have been developed for grouping water resources into discrete categories for various purposes based on similarity of chemical, biological, hydrological, morphological, geological, and geographical attributes of the water bodies or their catchments (the area draining directly to the lake). An example is the Strahler stream numbering system used to distinguish headwater streams from larger streams and rivers (Horton, 1945; Strahler, 1952; Strahler, 1957). Classification systems for lakes have focused on their relative position among other lakes in a flow network (Riera et al., 2000) or hydrodynamics (Winter, 1977). Various abiotic factors can be used to describe mountainous locations, including relative elevation, relief, and landscape position within drainage networks (Körner et al., 2011; Sayre et al., 2018). An approach based on these factors can be flexibly applied

across varied landscapes to capture mountain regions occurring at varying elevations.

In recognition of the importance of mountain lakes for habitat, water supply, and as centers of recreation and tourism, the goals of this study are: (1) develop a rigorous and repeatable classification system for “mountain” lakes (2) provide an overview of the characteristics of mountain lakes and (3) to estimate the condition of mountain lakes across the CONUS. To achieve this goal, we first develop a rules-based framework for classifying mountain lakes. We then leverage the United States Environmental Protection Agency’s (US EPA) National Lakes Assessment (NLA) to estimate the ecological condition of mountain lakes relative to non-mountain lakes. We characterize the patterns of human development near mountain lakes and examine how these development patterns may impact waterbodies in mountainous settings. Finally, we discuss the flexibility of our framework for classifying sub-populations of waterbodies and posit questions for further investigation about mountain lake condition and threats.

2. Methods

We begin by describing the NLA design, data collection, and assessment of condition. We then describe our process for classifying mountain lakes based on surrounding topography. Based on the resulting classification, we estimate the condition of the mountain lakes population and compare this to non-mountain lakes. Finally, we characterize the development patterns among the lakes sampled in the NLA to compare between mountain and non-mountain lakes.

2.1. National lakes assessment

US EPA’s National Aquatic Resource Survey (NARS) is a partnership between the EPA and state and tribal authorities to assesses the physical, chemical, and biological condition of waterbodies across the CONUS (<https://www.epa.gov/national-aquatic-resource-surveys>). The NARS includes the NLA, which quantifies the status and trends in the chemical, physical and biological condition of lakes by surveying a representative set of lakes (Herlihy et al., 2008; Peck et al., 2020) according to a probability-based survey design (Stevens and Olsen, 2003; Stevens and Olsen, 2004). As a result of the probability-based survey design, the status and trends in the broader population of the US can be inferred based on those sampled in the NLA. We chose the NLA for our analysis for three reasons: (1) it is the only existing survey that represents the broad population of lakes across the CONUS; (2) it includes lakes across the many mountainous regions of the CONUS, (3) the broad suite of data collected in the NLA allows us to investigate differences in ecological condition between mountain lakes and non-mountain lakes in the CONUS.

Each NLA samples approximately 1,000 lakes across size classes, nine aggregated ecoregions, and 15 hydrologic units (Herlihy et al., 2008; Peck et al., 2013). For the first NLA in 2007, the target population (i.e., population of interest) included all lakes at least 4 ha in surface area and at least 1 m deep. For the 2012 and all NLA since, the target population was expanded to include all lakes at least 1 ha in surface area and at least 1 m deep. Lakes are sampled once between June and September. At each site, field crews spend one day collecting a suite of data that capture the chemical, physical, and biological condition of each lake. The collection and analysis of these data are described in previous studies (Peck et al., 2013; Peck et al., 2020; Pollard et al., 2018; Yuan et al., 2014) and technical documentation (US EPA, 2011; US EPA, 2012). Briefly, a vertical profile and surface water samples for chemistry and phytoplankton are collected via boat at the deepest point in the lake. Assessment of the riparian and littoral habitat is conducted from 10 equally spaced locations around the lake perimeter. These data are summarized into key indicators that describe the overall lake condition.

For each indicator, a set of benchmarks or thresholds was developed

against which to evaluate the quality of the lake with respect to a given indicator. Some indicators are measurements of a single data type, and others are indices that integrate multiple data types into a composite metric. Indicators are categorized using benchmarks that are based either on established guideline values or the distribution of data for the indicator for selected minimally disturbed or reference site locations (Peck et al., 2020; Stoddard et al., 2006). For the latter, condition thresholds were developed using a reference condition approach. Briefly this approach uses the 5th and 25th (or 95th and 75th) percentiles of the distribution of the indicator scores in a set of regional reference sites. Based on the value of the percentiles, all sampled sites were assigned to good, fair, or poor condition based on these thresholds (see US EPA, 2017 for details).

Total phosphorus is an example of an indicator with benchmarks that are determined based on regional reference sites. Higher phosphorus is associated with poorer condition. For this indicator, total phosphorus concentration from reference sites within a region is used to calculate the 75th and 95th percentiles (Fig. S1). The 75th percentile is the boundary between good and fair condition while the 95th percentile is the boundary between fair and poor condition. These benchmarks are then used to assign condition categories to all lakes sampled with the region. Benchmarks are developed within nine regions of the CONUS that maximize within-region ecological similarity (Herlihy et al., 2008; Stoddard et al., 2008). As a result, the thresholds between condition categories can be different among regions.

For this analysis, we use the NLA conducted in 2007, 2012, and 2017. The total number of unique lakes was 2,251 because some lakes are sampled in multiple survey years. We use 12 of the survey indicators for this analysis: Three biological indicators (trophic status, chlorophyll *a*, benthic macroinvertebrates), four physical indicators (littoral cover, riparian vegetation cover, lake habitat complexity, and lakeshore disturbance), and five chemical indicators (acid neutralizing capacity (ANC), dissolved oxygen, total nitrogen, total phosphorus, and microcystins). Other indicators including atrazine and zooplankton were not collected in 2007 or used substantially different methods from the 2012 and 2017 NLAs and therefore not included in this analysis.

2.2. Classifying mountain lakes

We classified mountain lakes based on the extent of mountainous landforms within a given area around each lake. We classified mountainous areas using the USGS Landforms data that categorizes the CONUS into 10 distinct landforms at 30 m pixel resolution (Sayre et al., 2009a). The landscape of the CONUS is sorted into landforms based on slope and relief characteristics (drainage channels, flat plains, smooth plains, irregular plains, escarpments, low hills, hills, breaks/foothills,

low mountains, and high mountains/deep canyons) (Sayre et al., 2009b). Two of these categories (low mountains and high mountains/deep canyons) were used here to classify mountainous areas. There were two sequential steps to the analysis to categorize lakes as either mountain or non-mountain: determining (1) the extent of area around the lake to be considered and (2) the proportion of that area within the extent that is categorized as mountainous (Fig. 1).

For the first component, extent, we considered the area draining directly to the lake, referred to here as the lake catchment. In contrast, the lake watershed includes the entire upstream drainage area. We chose the catchment for the extent rather than the entire watershed because it captures immediate surroundings of the lake and represents direct mountainous influence on the lake ecosystem. We opted not to use the lake watershed since the watershed for many lakes in the NLA extends over large areas and can encompass many upstream lakes that have the capacity to transform conditions from snow-dominated headwater regions to lowland valleys (Pollard et al., 2018). Here, we use the catchment definition developed for LakeCat, a framework for associating geospatial data with lakes across the CONUS (Hill et al., 2018). In this framework, separate methodologies are used for lakes that are connected to the river and stream flow network (on-network lakes) and lakes that lack flowline connections (off-network lakes). For on-network lakes, the lake catchment is defined as any area draining to the specific lake that is not first routed through upstream stream or river flowlines, and more specifically, it is the catchment or set of catchments that intersect with the lake and share a linking identifier with the lake in NHDPlusV2 (McKay et al., 2012). For off-network lakes, the catchment is defined topographically as any area that drains to a lake and excludes areas that drain to topographically upslope lakes. For both on- and off-network lakes, the catchment area excludes area that drains to upstream lakes. See Hill et al. (2018) for detailed methodology. In this analysis, the lake area is excluded from the catchment area. For the sampled NLA lakes, the mean distance between the lake boundary and the catchment boundary had a median of 530 m with 95 % of distances between 76 m and 3,653 m.

For the second analysis component, we calculated the proportion of the lake catchment comprising mountain terrain and used this to classify lakes as either mountain or non-mountain. We explored several different proportion thresholds. We chose to use a proportional threshold to account for the large range in sizes of lake catchments from the NLA. To inform the threshold used for this analysis, we compiled studies of lakes that were referred to as “mountain lakes” or were characterized as occupying a “mountain ecosystem”. Our goal is to identify a threshold that is inclusive of commonly studied mountain lakes. Studies were selected to represent different mountain regions in the US. We processed these example lakes using the above framework to derive the proportion

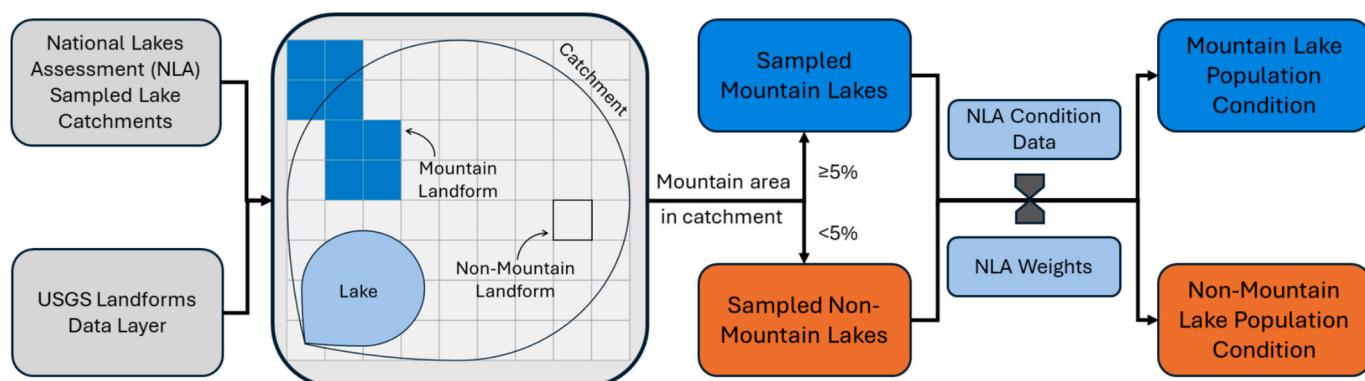


Fig. 1. Schematic diagram of lake classification process. The catchments for the lakes sampled in the 2007, 2012, and 2017 NLAs are overlaid the USGS landforms data to extract the percent of the catchment that is mountain landform. If the proportion mountain area exceeds a chosen percentage threshold, the lake is classified as a mountain lake. If below the threshold, the lake is considered a non-mountain lake. The NLA condition data and sample weights are applied to estimate the condition of all mountain and non-mountain lakes in the CONUS target population (> 1 ha surface area and > 1 m deep).

of the catchment that is mountain terrain. We then chose a threshold based on this analysis that would be inclusive of these example systems. In addition, we tested the thresholds of 1, 5, 10, and 25 % mountainous area within the catchment to explore how the chosen threshold would impact the number of sampled lakes, the estimated population size, and estimated condition of the population for both mountain and non-mountain lakes.

2.3. Mountain lake characteristics

We provide an overview of mountain lake and associated catchment and watershed characteristics with particular attention to differences between eastern and western mountain regions in the CONUS. We extracted the percent mountain landform in the lake catchment, lake elevation, maximum lake depth, and lake area. In addition, for the lake watersheds we show the distribution of the watershed area, mean slope, and land cover including developed, agricultural, forest, and perennial snow and ice (see Table S1 for data sources and citations). We compare lake origin, a metric developed by the NLA to determine which sampled lakes were present prior to European settlement (naturally occurring) versus after European settlement (artificially constructed) (Whittier et al., 2002; US EPA, 2022), among mountain and non-mountain lakes.

To investigate the patterns of human development near lakes, we compare the percent developed area in the watershed and catchment of mountain and non-mountain lakes. We calculated the amount of low, medium, and high intensity development from the National Land Cover Database (NLCD, Dewitz and U.S. Geological Survey, 2021) from 2011 within the lake catchments and watersheds. We used the protected areas database of the US to quantify the proportion of mountain and non-mountain lake catchments that are within the boundaries of National Forest Land and designated Wilderness Areas, and therefore, in regions with restricted development (U.S. Geological Survey, 2024). We used the Microsoft Building Footprints (Microsoft, 2018) as an additional, more detailed measure of development in the catchment and watershed of lakes. The Microsoft Building Footprints can provide higher resolution information about buildings in low development areas (Huang and Jin, 2022).

Finally, we explored several characteristics of mountain lakes that would make them potentially more vulnerable to the impacts of human development. We compared the mean slope, runoff, hydraulic conductivity, and depth to bedrock between mountain and non-mountain lake catchments.

2.4. Mountain lake condition

After developing the classification scheme above for mountain and non-mountain lake categories, estimates of condition were calculated to apply to lake populations in the CONUS. We generated waterbody condition estimates using the NLA design (Peck et al., 2013; Pollard et al., 2018) and the *spsurvey* package (Dumelle et al., 2023a). The indicator data and survey design weights are combined to estimate population parameters and, more broadly, develop complete characterizations of the target population (Dumelle et al., 2023b). We estimated the number of lakes falling into condition categories for mountain lakes, non-mountain lakes, and all lakes in the CONUS by evaluating the percent of lakes and number of lakes falling into good, fair, and poor categories for the biological, chemical, and physical indicators. All data analysis was conducted in the R programming environment (R Core Team, 2023).

3. Results

3.1. Mountain lakes in the conterminous US

In the NLA, 1,781 sampled lakes (79.1 %) have no mountainous terrain within their lake catchment. Among the 470 lakes (20.9 %) that

have some mountainous terrain, the percent mountainous area ranges from < 0.01 % to 100 % (median = 39.7 %). Based on the four tested thresholds for mountainous terrain, the number of NLA lakes identified as mountain lakes ranged from 447 lakes for the 1 % mountain area threshold to 316 lakes with a 25 % mountain area threshold (Table 1). Extrapolating to the CONUS population, the estimated mountain lake population size ranged from 13,450 (11,539–15,360) lakes for the 1 % mountain area to 10,235 (8,585–11,884) lakes for the 25 % threshold. Notably, the different thresholds had a much smaller impact on the size of estimated non-mountain lake population. The estimated non-mountain lake population size ranged from 180,203 (164,914–195,493) for the 1 % mountain area threshold to 183,418 (168,047–198,789) lakes for the 25 % threshold. In other words, the population size difference for 1 % versus a 25 % threshold results in a 29 % decrease in the number of mountain lakes versus a 2 % increase in the number of non-mountain lakes. In addition, the mountain area threshold had only a marginal impact on the estimated condition of mountain and non-mountain lake populations (Fig. S2).

To help inform a threshold of mountain terrain that would capture many mountain lakes across the CONUS, we reviewed 19 lakes from previous studies that are identified as “mountain lakes” from the literature (Table 2). These included 14 lakes in western states and 5 lakes in eastern states. The proportion of mountain area in the catchments of these example lakes ranged from 0 to 100 % (median = 49 %). One of the 19 studied lakes (Upper Lake Mary in Arizona) was excluded for containing no mountain terrain in the catchment. Emerald Lake had the lowest percent mountain area that was greater than zero (9 % mountain area). To be inclusive of these commonly studied and cited mountain lakes across the western and eastern portions of the CONUS and to expand on analyses that have historically only included high elevation and alpine lakes, we selected a mountain area threshold of 5 % for this study.

Based on the 5 % threshold for mountain area within the lake catchment, 410 (18 %) of the 2,251 lakes sampled in the 2007, 2012, and 2017 NLA were classified as mountain lakes (Fig. 2). Mountain lake catchments have a median of 48 % mountain area. Based on the 5 % threshold for mountainous terrain in the lake catchment, there are an estimated 12,353 (10,529–14,177) mountain lakes in the CONUS that are at least 1 ha in surface area and 1 m deep compared with 181,300 (165,996–196,604) non-mountain lakes. As a proportion, mountain lakes account for an estimated 6.7 % of lakes in the CONUS.

Most mountain lakes are west of the Mississippi River ($n = 337$) with only 73 lakes east of the river. Sampled western mountain lakes tend to occur at higher elevations, have steeper mean slopes, and have a higher proportion of their catchment that are mountain landform than lakes in the east (Fig. 3). Western and eastern mountain lakes are comparable in terms of maximum lake depth, lake area, and watershed area with western mountain lakes having a slightly higher maximum range. Western mountain lakes have lower forest cover compared to eastern

Table 1

The number of NLA sampled lakes and the estimated population size of mountain or non-mountain lakes based on different thresholds of mountain area within the lake catchment. Estimated populations refer to lakes of >1 ha and >1 m deep in the conterminous US.

Threshold	Mountain Lakes		Non-Mountain Lakes	
	NLA Sampled	Estimated Population (95 % CI)	NLA Sampled	Estimated Population (95 % CI)
1 %	447	13,450 (11,539–15,360)	1804	180,203 (164,914–195,493)
5 %	410	12,353 (10,529–14,177)	1841	181,300 (165,996–196,604)
10 %	388	11,314 (9,600–13,027)	1863	182,339 (167,024–197,655)
25 %	316	10,235 (8,585–11,884)	1935	183,418 (168,047–198,789)

Table 2

Mountain lakes identified in the literature and the percent mountain terrain within the lake catchment.

Lake Name	State	Mountain Range	Mountain Landform (%)	Citation
Bubb Lake	NY	Adirondack	32	(Driscoll et al., 2003)
Heart Lake	NY	Adirondack	47	(Driscoll et al., 2003)
Mountain Lake	VA	Appalachian	28	(Roningen and Burbey, 2012)
Beartooth Lake	WY	Beartooth	82	(Williamson et al., 2010)
Mowich Lake	WA	Cascade	92	(Brittain and Strecker, 2018)
Crater Lake	OR	Cascade	76	(Larson et al., 2007)
Rondout Reservoir	NY	Catskill	29	(McHale et al., 2017)
Lake Powell	AZ	Colorado Plateau	40	(Stanford and Ward, 1991)
Hoh Lake	WA	Olympics	100	(Sheibley et al., 2014)
The Loch	CO	Rocky	81	(Baron et al., 2021)
Sky Pond	CO	Rocky	78	(Baron et al., 2021)
Flathead Lake	MT	Rocky	42	(Xiong et al., 2022)
Upper Lake Mary	AZ	San Francisco	0	(Button and Blinn, 1975)
Coeur d'Alene Lake	ID	Sellirk & Coeur d'Alene	44	(Horowitz et al., 1995)
Lake Tahoe	CA	Sierra Nevada	49	(Vander Zanden et al., 2003)
Emerald Lake	CA	Sierra Nevada	9	(Sadro et al., 2011)
Castle Lake	CA	Siskiyou	81	(Goldman, 1961)
Upper Carroll Lake	UT	Uinta	91	(Hundley et al., 2016)
Mirror Lake	NH	White	64	(Likens, 2000)

mountain lakes. None of the sampled eastern mountain lake watersheds contain perennial snow or ice cover compared to 20 % of western mountain lakes. Approximately half of sampled mountain lakes are naturally occurring (49 %) versus artificially constructed (51 %). Slightly fewer non-mountain lakes were naturally occurring (45 %) versus artificially constructed (55 %). Mountain lakes often lie in federally protected areas, with 57 % of mountain lake catchments on National Forest land and 22 % in National Wilderness Areas. In contrast, just 7 % and 2 % of non-mountain lake catchments occur in National Forest and Wilderness Areas, respectively. Both western and eastern mountain lakes are low in agricultural and developed land cover; however, the patterns in development differed for mountain lakes and non-mountain lakes, as described below.

While mountain lakes of the CONUS are in less developed regions, development is still present around some lakes. In addition, mountain lakes have characteristics that may increase their vulnerability to impacts from development. Based on building footprints, 41 % of mountain lake catchments are free of buildings compared to only 20 % of non-mountain lakes. In addition, among mountain lakes that did have buildings in the catchment, the median number of buildings is 26 and approximately half the median of 48 for non-mountain lakes. Mountain lakes also had lower mean percent developed land cover within their catchments and watersheds (Fig. 4). Developed land cover within the catchment area is slightly higher for both mountain and non-mountain lake catchments compared to the watershed. When evaluating the ratio of catchment to watershed percent area developed, mountain lakes have a higher mean ratio (2.8 ± 0.2) compared to non-mountain lakes (1.5 ± 0.1). Finally, mountain lakes differ in several characteristics that

may contribute to how development can impact these systems. Mountain lake catchments have lower soil hydraulic conductivity, higher annual runoff, and shallower depths to bedrock compared to non-mountain lakes (Fig. 5).

3.2. Condition of mountain lakes

For 11 of 12 indicators, mountain lakes are in better condition compared to both non-mountain lakes (Fig. 6) and the population of lakes in the CONUS as a whole (Fig. S3). Since the population of all lakes includes mountain lakes, we present the results in terms of mountain lakes versus non-mountain lakes for ease of presentation and interpretation. A higher proportion of mountain lakes are in good condition (range: 46.3 % to 93.1 %) compared to non-mountain lakes (17.5 % to 78.1 %) for 11 indicators. The one exception was acid neutralizing capacity, with 92.8 % of mountain lakes in good condition compared to 97.7 % of non-mountain lakes. For all indicators, a smaller proportion of mountain lakes are in poor condition (0.0 % to 32.8 %) compared to non-mountain lakes (1.0 % to 53.2 %).

Among biological indicators, the trophic status of nearly half of mountain lakes is oligotrophic compared to under 10 % of non-mountain lakes (Fig. 6). In contrast, eutrophic or hypereutrophic mountain lakes were less common than among non-mountain lakes. Chlorophyll *a* and benthic macroinvertebrates are in good condition for over half of mountain lakes, respectively, versus less than half of non-mountain lakes.

Among the physical habitat indicators, a high percent of mountain lakes were in good condition for littoral cover and lake habitat complexity compared to non-mountain lakes (Fig. 6). Riparian vegetation and lakeshore disturbance were the two indicators with the lowest proportion of mountain lakes in good condition; however, this is still higher than the proportion for non-mountain lakes.

Among the chemical indicators, dissolved oxygen is in good condition for over 90 % of mountain lakes compared to just over 75 % for non-mountain lakes (Fig. 6). Acid neutralizing capacity is the single indicator for which mountain lakes had a lower proportion in good condition compared to non-mountain lakes. For total nitrogen and total phosphorus, nearly double the proportion of mountain lakes are in good condition compared to non-mountain lakes. Finally, microcystin detection is far less prevalent in mountain lakes compared to non-mountain lakes.

4. Discussion

While mountain lakes are important resources, there has not yet been a comprehensive survey of these ecosystems in the CONUS. Prior to the NLA, there were just two national surveys of lakes in the US. The first was the National Eutrophication Survey that focused on lakes with point sources of nutrient pollution (US EPA, 1975) and therefore excluded most mountain lakes. The second was a survey of the impact of acid rain on waterbodies that were poorly buffered and disproportionately included mountain lakes (Eilers et al., 1986; Landers et al., 1988). The NLA is the first survey that focuses on all lakes in the CONUS and, as a result, makes an analysis of this specific subpopulation possible. Based on the NLA, we find that mountain lakes are in better condition than non-mountain lakes with respect to most indicators of physical, chemical, and biological condition. Yet, mountain lakes are not without environmental concerns and sensitivities.

4.1. Mountain lakes as a subpopulation

One of the challenges to assessing the status of mountain lakes is classifying lakes as mountainous versus non-mountainous. Elevation is inadequate due to elevated plateaus that lack mountains while steep coastal ranges occur near sea level. In this study, we used local landforms to be inclusive of mountain lakes in the eastern and western

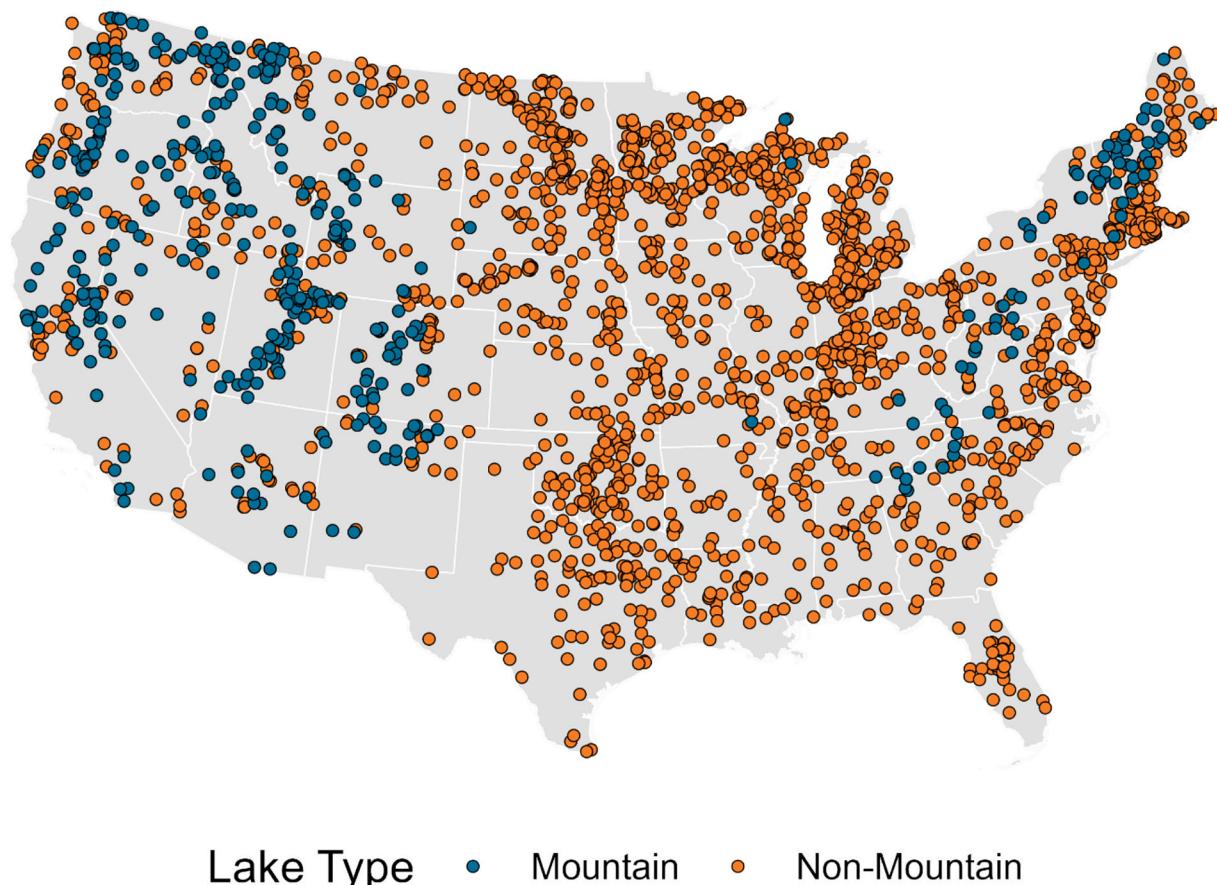


Fig. 2. Lakes sampled in the 2007, 2012, and 2017 National Lakes Assessment. Mountain lakes are identified as having $\geq 5\%$ mountain landform within their catchment. For easier viewing, mountain lake (in blue) dots are shown on top of the more abundant non-mountain lakes (in orange).

regions of the CONUS. Indeed, we found that eastern mountain lakes occurred at a mean elevation of just 360 m compared to western mountain lakes occurring at a mean of 1,730 m. For comparison, using a 3,000 m (10,000 ft) cutoff for alpine lakes would have only included 41 NLA sampled lakes in the CONUS, eliminating all eastern and most western lakes from the analysis. In addition, numerous studies on the impacts of acid rain deposition focused on remote mountain lakes (Driscoll et al., 2007; Marchetto and Rogora, 2004; Patrick et al., 1998). In contrast, our approach is agnostic to access and protection status thereby allowing us to assess development patterns across the broadly defined subpopulation.

4.2. Mountain lake condition

Mountain lakes are in better condition than non-mountain lakes in the CONUS for almost every indicator. An exception to this is ANC, for which a higher proportion of non-mountain lakes are in good condition compared to mountain lakes. Surface waters in mountainous areas are often relatively poorly buffered, and were disproportionately affected by acid deposition, although following implementation of the Clean Air Act amendments of 1990, acidification and its effects have often been at least partially reversed in mountain lakes and streams of the eastern US (Baldigo et al., 2015; Baldigo et al., 2021; Burns et al., 2006; Driscoll et al., 2016). The lower ANC seen in lakes at higher elevation has been noted and variously attributed to relatively steep slopes, thin soils, unvegetated terrain, and slower rates of bedrock weathering (Berg et al., 2005; Burns et al., 2006; Melack et al., 1985; Nanus et al., 2009; Sullivan et al., 2007). Bedrock weathering, and the corresponding geogenic production of free base cations (an important component of ANC), is expected to be slower in areas underlain by low-solubility, siliceous

sedimentary or felsic igneous (e.g., granitic) rocks, and higher in areas underlain by limestone or metamorphic rocks (Burns et al., 2006; Clow et al., 2010; Clow and Sueker, 2000; Melack et al., 1985; Nanus et al., 2009; Shaw et al., 2013; Staufer, 1990). Lakes that have been historically impacted by acid deposition which has abated in recent years are generally located in the eastern US and may experience delayed ecological improvement (Baldigo et al., 2015; Baldigo et al., 2021).

While the CONUS mountain lakes are in overall better condition than non-mountain lakes, a substantial proportion of the mountain lake population has challenges with respect to nutrients, trophic status, biological communities, and physical habitat. This is partially a consequence of the inclusion of lakes at lower elevations that are more accessible compared to more remote mountain and alpine lakes that have historically been the focus of other studies (Catalan et al., 2009b; Moser et al., 2019). Over a third of mountain lakes are in fair and poor condition for total nitrogen and phosphorus. This may be in part a result of residential septic systems leaching nutrients to nearby waterbodies (Withers et al., 2014). In addition, elevated nutrients may be due in part to increased atmospheric deposition in some mountain ranges with greater development in adjacent regions and increased dust transport (Baron et al., 2011; Brahney et al., 2015). Additionally, as the climate continues to warm in mountain regions, increasing soil temperatures can result in higher phosphorus leaching (Scholz and Brahney, 2022). The greater availability of nutrients in some mountains likely contributes to 25 % of mountain lakes being classified as eutrophic or hypereutrophic, indicating high primary productivity. While mountain lakes seem unlikely candidates for harmful algal blooms, there are some mountain lakes where harmful algal blooms occur regularly due in part to relatively high phosphorus (Jansen et al., 2024).

One third of mountain lake benthic macroinvertebrate communities

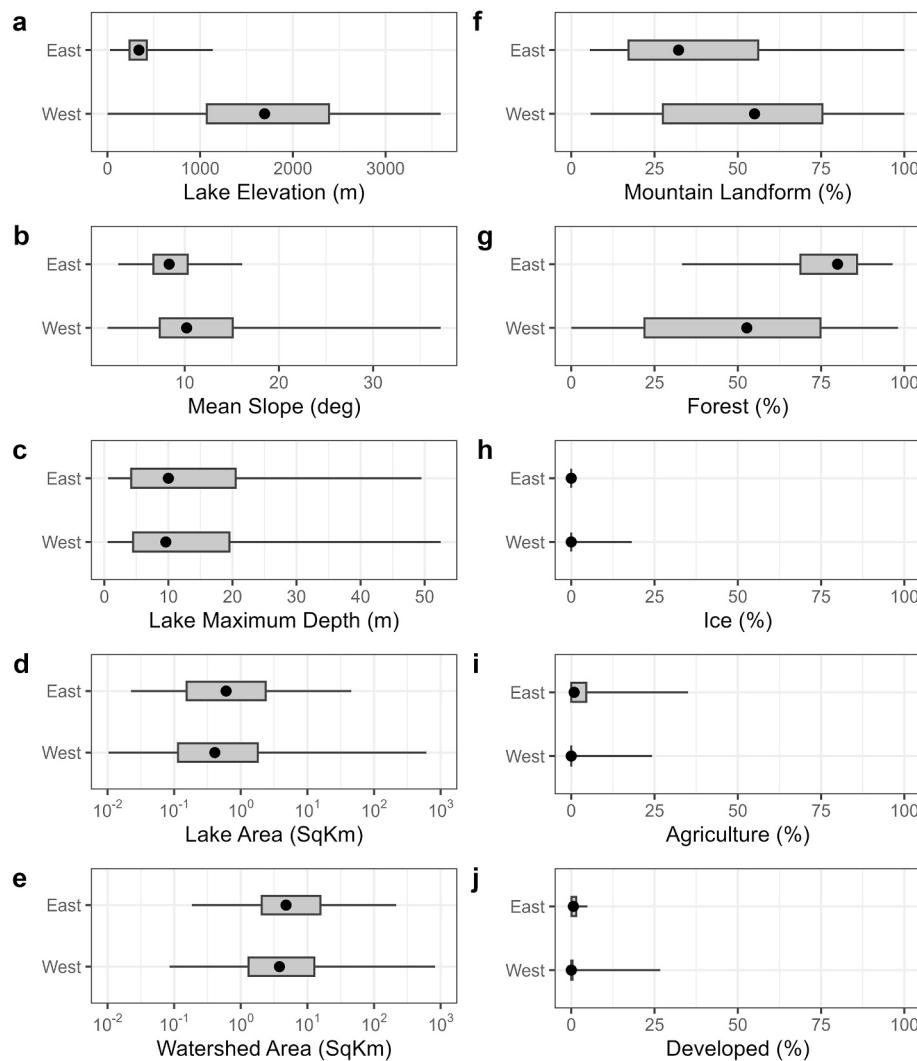


Fig. 3. Boxplots of mountain lake characteristics in the eastern and western United States. The lake elevation (a), catchment mean slope (b), lake maximum depth (c), lake surface area (d), watershed area (e), as well as percent mountain landform in the catchment (f) and amount of forest (g), ice (h), agriculture (i), and developed (j) land cover in the lake watersheds. Boxes represent the 25th and 75th percentiles, whiskers show the full data range, and circles indicate the mean.

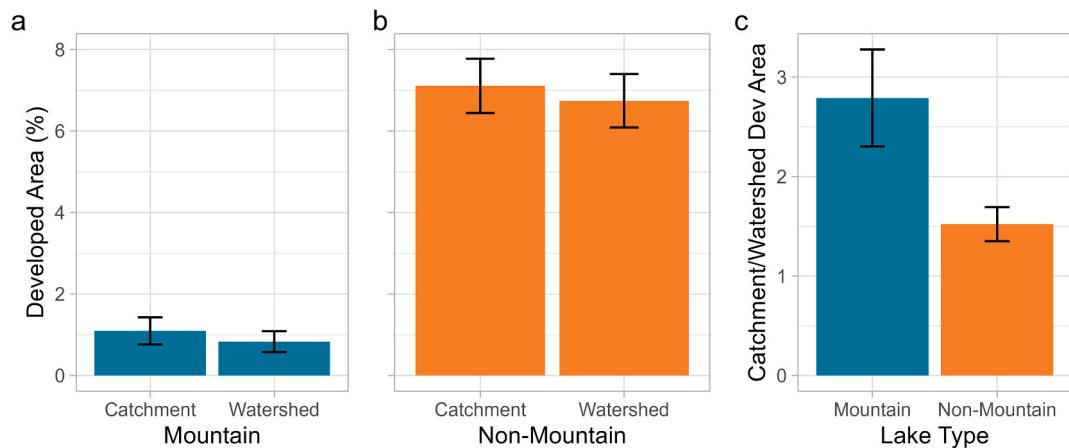


Fig. 4. The mean \pm 95 % confidence interval of percent of low, medium, and high intensity development land cover in mountain (a) and non-mountain (b) lake catchment and watershed areas. The mean ratio of the catchment to watershed developed area for mountain and non-mountain lakes (c).

are in fair or poor condition. The impaired conditions of these sensitive taxa may be in due part to the previously mentioned delayed recovery from acidification in some areas. Another pathway is the introduction of

non-native fish to numerous historically fishless mountain lakes (Eby et al., 2006). Many of these fish species, such as rainbow trout, predate heavily on benthic macroinvertebrates at least for a period of their life

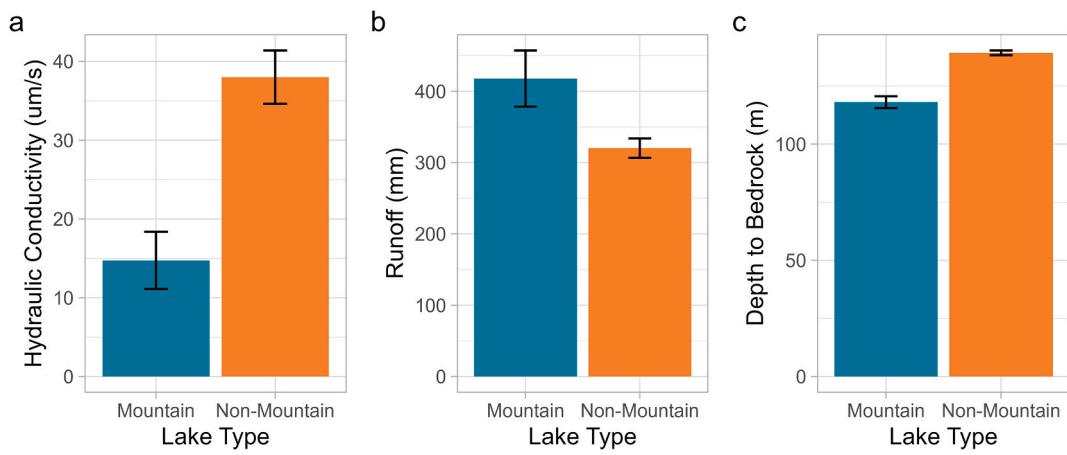


Fig. 5. The mean \pm 95 % confidence interval of the soil hydraulic conductivity (a), annual runoff (b), and depth to bedrock for mountain and non-mountain lake catchments.

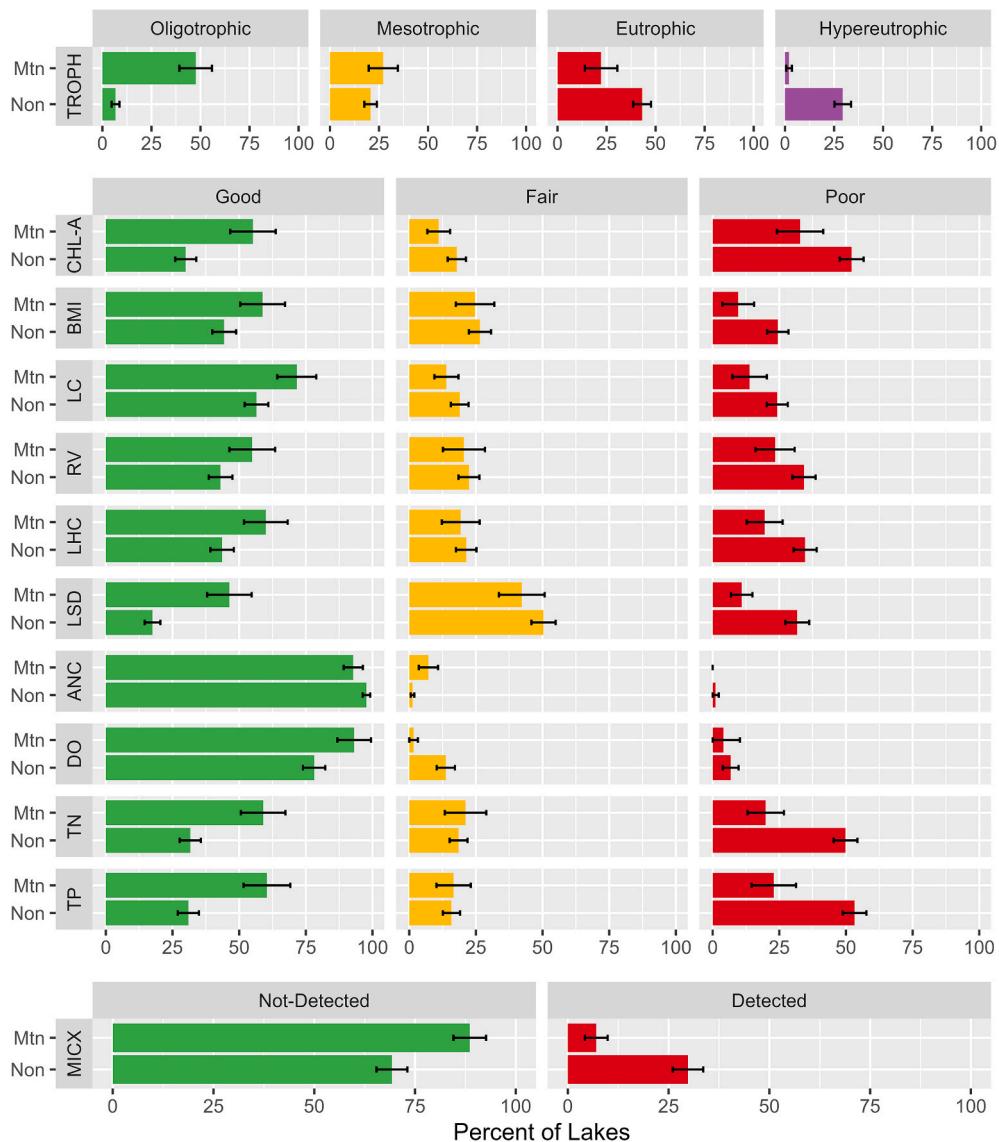


Fig. 6. The mean estimate and 95% confidence interval of the proportion of the population within each condition category for mountain (Mtn) and non-mountain (Non) lakes for the conterminous US with respect to trophic status (TROPH), chlorophyll-a (CHL-A), benthic macroinvertebrates (BMI), littoral cover (LC), lake habitat complexity (LHC), riparian vegetation (RV), lakeshore disturbance (LSD), acid neutralizing capacity (ANC), dissolved oxygen (DO), total nitrogen (TN), total phosphorus (TP), and microcystin (MICX).

span (Eby et al., 2006). The decline in many lake benthic macro-invertebrates, especially large-bodied taxa, following fish stocking has been observed in multiple mountain ranges (Schilling et al., 2009). Management agencies like the National Park Service are currently mitigating these impacts by removing fish where possible (Chiapella et al., 2018; Schilling et al., 2009). An additional stressor to the littoral benthic invertebrates is the disturbance of the lakeshore. Anthropogenic development of the lakeshore can substantially reduce the productivity and diversity of benthic macroinvertebrates along with altering other biotic communities (Pätzig et al., 2018).

4.3. Mountain lake vulnerability to human development

Although mountain lakes as a population are in better condition relative to non-mountain lakes, more than 50 % of mountain lakes are in fair or poor condition with respect to lakeshore disturbance. While many mountain lakes are in remote settings that limit development and lakeshore disturbance, when including a broader set of mountain lakes such as those occurring in lower-lying mountain ranges, many of these lakes are experiencing substantial lakeshore disturbance.

Mountain lakes have lower proportions of development within the whole watershed compared to non-mountain lakes; however, there is more than twice the percent developed land in mountain lake catchments compared to within the whole lake watershed (Fig. 4). This is consistent with other research demonstrating that development pressures in mountain and alpine systems are substantial. Mountain developments for tourism and hydropower negatively impact lake water quality as well as aesthetics value (Ebner et al., 2022b; Pastorino et al., 2024; Schirpke and Ebner, 2022). Tourism can have a variety of impacts from increased litter to increased sediment loading from road construction (Dokulil, 2014). Furthermore, agriculture within the watershed of oligotrophic mountain lakes can negatively affect water quality through sediment and nutrient runoff while agriculture in adjacent watersheds can negatively affect water quality through atmospheric nutrient deposition (Brahney et al., 2015; Fuhrer et al., 2014). Lower elevation lakes and those outside of protected areas are especially vulnerable to increasing development impacts into the future (Schirpke and Ebner, 2022). Even mountain lakes within protected areas and remote locations are vulnerable to impacts from recreational development and use (Ebner et al., 2022a; Ebner et al., 2022b; Pastorino et al., 2024; Schirpke and Ebner, 2022; Senetra et al., 2020). In summary, mountain lakes, while often more remote than non-mountain lakes, can still be impacted by direct human development.

Mountain lake catchment characteristics may make these systems more vulnerable to lakeshore disturbance from human development compared to non-mountain lakes. The steeper slopes and higher runoff in mountain lake catchments facilitates the flow of pollutants from developed areas to the lake water. This is consistent with studies that have found a relationship between higher slopes and nutrient concentrations in mountain lakes (Kamenik et al., 2001; Sadro et al., 2012). The lower hydraulic conductivity likely indicates lower soil infiltration. When infiltration does occur, there is less soil to store and retain pollutants and sediments, as indicated by shallower depths to bedrock. Taken together, mountain lake catchments may on average convey the pollutants from developed areas more quickly to the lake water with few opportunities for attenuation. Future work should focus on determining how development influences mountain lake condition.

While this analysis focused on characterizing the condition of mountain lakes at a broad, CONUS scale, a promising area of future research is to link environmental drivers to individual mountain lakes using modeling approaches such as machine learning algorithms (James et al., 2013) like random forests (Breiman, 2001) or spatially explicit statistical models that incorporate spatial dependence (Cressie, 1993; Dumelle et al., 2023a; Zimmerman and Ver Hoef, 2024). Such approaches can help build predictive models that can identify individual mountain lakes across the country that have specific water quality

challenges.

5. Conclusion

This study solves two problems that build on one another. First, we developed a rules-based approach to classify lakes by landform. Second, this study presents a comprehensive evaluation of the condition of mountain lakes across the CONUS. The process we developed for classifying lakes is flexible and can be adapted to classify waterbodies or even other environmental resources for a variety of purposes by altering the data and spatial extent components of the framework. Our findings reveal that mountain lakes are in better physical, chemical, and biological condition compared to non-mountain lakes across most indicators. However, there are significant environmental challenges within the mountain lake population, including high nutrient levels and eutrophic conditions in a notable proportion of these waterbodies. This study underscores the vulnerability of mountain lakes to human development, particularly near lakeshores. Concentrated lakeshore development, combined with inherent edaphic characteristics such as high runoff and low hydraulic conductivity, heightens the risk of pollutant transfer to mountain lakes. These findings highlight the need for targeted conservation and management strategies to mitigate human impacts and preserve the ecological integrity of mountain lakes, particularly along the lakeshore. With 1.9 billion people living in or directly downstream of mountainous areas (Immerzeel et al., 2020), these water towers of the planet (Messerli et al., 2004) merit research and management. Future research should focus on the mechanisms driving nutrient enrichment and the impact of lakeshore development, informing more effective strategies to protect these vital ecosystems.

CRediT authorship contribution statement

Amalia M. Handler: Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Conceptualization. **Marc Weber:** Writing – review & editing, Methodology, Formal analysis, Conceptualization. **Michael Dumelle:** Writing – review & editing, Methodology, Formal analysis, Conceptualization. **Lara S. Jansen:** Writing – review & editing, Writing – original draft, Methodology, Conceptualization. **James N. Carleton:** Writing – review & editing, Writing – original draft. **Blake A. Schaeffer:** Writing – review & editing, Writing – original draft, Conceptualization. **Steven G. Paulsen:** Writing – review & editing, Conceptualization. **Thomas Barnum:** Writing – review & editing, Conceptualization. **Anne W. Rea:** Writing – review & editing, Conceptualization. **Anne Neale:** Writing – review & editing, Conceptualization. **Jana E. Compton:** Writing – review & editing, Supervision, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2025.113402>.

Data availability

Data and code for this analysis is available at Data.gov via <https://doi.org/10.23719/1532058>.

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