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The Vulnerability of Littoral Structures Under Multiyear Drought Conditions

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THE VULNERABILITY OF LITTORAL STRUCTURES

UNDER MULTIYEAR DROUGHT CONDITIONS

by

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ABSTRACT

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Utah State University, 2019

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Multiyear drought is a threat to ecological, municipal, and agricultural water demands across the globe. As lake levels decline during drought, the associated downslope shift of littoral zones can reduce riparian linkages and availability of littoral structure essential for the persistence and growth of aquatic biota. Here, I quantify the vulnerability of littoral structure (cobble, coarse woody habitat, and aquatic vegetation) across the conterminous United States under drought conditions. I use the EPA's National Lakes Assessment to analyze the physical habitat characteristics of 1,018 lakes and reservoirs sampled in 2012, when ~75% of the nation experienced drought. We calculated the probability of littoral structure loss for cobble and coarse woody habitat loss as well as the probability of absence for aquatic vegetation as lake levels decline under drought conditions using a logistic mixed-effect modeling framework. Our results suggest cobble and coarse woody habitat were particularly vulnerable regardless of the magnitude of lake level decline. Similarly, the probability of aquatic vegetation absence increases as lake levels decline, though to a lesser degree than other littoral structures. From reduced macroinvertebrate diversity to degraded fisheries, the consequences of littoral structure loss can cascade through entire ecosystems. Our results highlight the vulnerability of littoral structures across the United States in the face of multiyear drought conditions.

(63 pages)

PUBLIC ABSTRACT

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Climate change is associated with altered environmental conditions and shifting mosaics of suitable habitats for organisms. Climate change in the form of drought can shift important lake shoreline habitats downslope, altering the lakes chemistry and habitat availability. Additionally, negative biological consequences can occur after a loss of submerged habitat along shorelines, hereafter littoral habitat. The objective of this study is to evaluate whether littoral habitat is lost (cobble, coarse woody habitat (fallen trees; CWH), and aquatic vegetation) under drought conditions across the United States. I used the National Lakes Assessment physical habitat data collected in summer 2012, when 75% of the U.S. experienced drought. I calculated the probability of cobble, CWH, and aquatic vegetation loss with lake level decline. I found cobble and CWH were highly vulnerable, where just 1 meter of lake level loss would result in nearly 100% habitat loss. Aquatic vegetation exhibited vulnerability but at a higher threshold. Multiyear drought will continue into the future with scientists estimating increases in drought frequency and severity, and we do not yet understand how or if aquatic animals will be resilient to a loss of littoral habitat. For example, previous research suggests food webs may be slow to recovery following littoral habitat loss. We must continue to evaluate the biological and environmental consequences of littoral habitat loss under drought conditions to successfully manage lakes and reservoirs into the future.

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CHAPTER I

INTRODUCTION

Ecological disturbance is often defined by scientists, resource managers, and lawmakers as “drastic deviations away from a natural state,” (White & Picket, 1985; Huston, 1994). Drivers of ecological disturbance can span spatial and temporal scales. Some disturbances arise over slow time scales, such as anthropogenic climate change, while others occur quickly, like storms or grazing (Naiman & Turner, 2000). For example, in arid and semi-arid regions, climatically-influenced multiyear drought is a regional disturbance that can have lasting effects over time and space (Bates *et al.,* 2008; Seager & Vecchi 2010; Lake, 2011). Regional, local, slow, or quick, disturbances have the potential to alter natural environments with effects ramifying through food webs and ecosystems (Naiman & Turner, 2000). Spatial and temporal ranges of global ecological disturbances vary widely, and so too does our understanding of resulting social and environmental consequences (Rogers, 1996; Millennium Ecosystem Assessment (MEA), 2005).

Aquatic ecosystems are particularly vulnerable to disturbance; many lakes exhibit changes through climate change and land use, which is especially concerning considering freshwater aquatic ecosystems only make up a small fraction of water on earth (Sala *et al.,* 2000; Carpenter *et al.,* 2011). The disturbances that occur in these environments are often anthropogenically-derived, such as land use change (Vitousek, 1994), habitat loss (Fagan, 2002), pollution (Medina *et al.,* 2007), and introduced invasive species (Sala *et al.,* 2000). Further, lentic systems are especially sensitive to climatically-influenced disturbance, such as drought, resulting in altered limnetic conditions (e.g., water level, salinity, and/or stratification) (Schindler, 2009). Many water bodies have also experienced a myriad of other stressors directly from human development (e.g., hydroelectric/water storage dams, irrigation withdrawals, and/or residential shoreline development) (Schindler, 2001; Carpenter *et al.,* 2011). Therefore, lentic ecosystems provide a compelling framework for understanding ecosystem disturbance.

Climate change-driven drought is a slow, regional disturbance with the potential to drastically alter lentic ecosystems. Drought represents a global threat to ecological, municipal, and agricultural water needs. Lake levels decline and littoral zones shift downslope as lakes and reservoirs dry up (Ficke *et al.*, 2007). This results in disconnectivity between riparian and littoral zones and the potential loss of cobble (Glassic & Gaeta, 2018), coarse woody habitat (Gaeta *et al.*, 2014), or aquatic vegetation (Dillingham *et al., in prep*), all of which can be essential for the persistence and growth of aquatic biota in littoral zones (Bowen *et al.*, 1998). A limited number of case studies have linked drought, littoral structure availability, and aquatic biota in specific lakes (e.g., Glassic & Gaeta 2019; Gaeta *et al.*, 2014); however, we do not know whether these patterns hold true across large spatial scales. Consequently, we need a deeper understanding of the scope and scale of lake level-driven loss of littoral structure across broad spatial scales, in order to anticipate potential future consequences of multiyear droughts under future climate change.

In Chapter 2, I quantified the effect of lake level decline under drought conditions on littoral structure loss in 1,018 lakes and reservoirs across the United States of America. My objective was to test whether various littoral structures (cobble, coarse woody habitat, aquatic vegetation) are vulnerable to lake level declines associated with drought using the National Lakes Assessment (NLA) database (USEPA, 2017). Climate change-driven drought is projected to occur more frequently and with longer durations into the future (Bates *et al.*, 2008; Seager & Vecchi 2010; IPCC, 2018). Therefore, identifying the relationships between multiyear drought, lentic water level, and littoral structure is a crucial step in understanding how lentic ecosystems might be affected by drought (Ficke *et al.*, 2007; Gaeta *et al.*, 2014).

CHAPTER II

THE VULNERABILITY OF LITTORAL STRUCTURES UNDER MULTIYEAR DROUGHT CONDITIONS

Introduction

Anthropogenic climate change is a global reality; however, the rate at which environmental changes will manifest in the future is highly uncertain (Karl & Trenberth 2003; Carpenter *et al.*, 2011; IPCC, 2018). From melting glaciers in the Arctic, to dwindling water supply in arid-region reservoirs, climate change will continue to shift the mosaic of suitable rearing, spawning, or foraging environments to which many aquatic organisms rely for population persistence (Schindler, 2009). Ultimately, such changes can be detrimental to the services ecosystems provide through impacts to native species or species of conservation concern, ecological and municipal water supply, and sustainable ecological processes such as food web stability or nutrient cycling (MEA, 2005). Climate change is diverse in its disturbance pathways: for example, higher precipitation can increase flooding and surpass sustainable reservoir storage, while lower precipitation and higher evapotranspiration leads to drought conditions, desiccating aquatic and terrestrial ecosystems alike (Barnett *et al.*, 2005; Mortsch & Quinn 1996; Lotsch *et al.*, 2005; Jung *et al.*, 2010). Indeed, climate change impacts vary spatially in severity and directionality cross the globe.

One particular concern in arid regions is consequences of the projected increase in drought frequency and severity on lentic ecosystems (Bates *et al.*, 2008; IPCC, 2018). Drought-driven alterations to hydrologic regimes manifest in lake level decline and decreased water volume, which is exacerbated by water withdrawal for human use, particularly on reservoirs (Coe & Foley, 2001). Reduced lake levels shrinks lakes and reservoirs (hereafter referred to as lakes) away from established shorelines, destabilizing the relationship between shallow lake perimeters (hereafter referred to as littoral zones) and the surrounding terrestrial ecosystem (Figure 1, Francis & Schindler, 2006; Penaluna *et al.*, 2018), potentially leaving littoral structures stranded along shorelines (Glassic & Gaeta, 2019; Gaeta *et al.*, 2014). However, this relationship depends on lake morphometry characteristics and the degree to which lake level declines. Such lentic habitat loss, not merely fragmentation, can have cascading effects on aquatic organisms that rely upon littoral structure in closed ecosystems during any stage of their life history.

Littoral structures are tremendously important to many lentic systems by stabilizing sediments (Gurnell *et al.*, 1995), concentrating nutrients (Schindler *et al.*, 1996), and providing favorable prey refuge (Nowlin *et al.*, 2004; Sass *et al.*, 2006b; Roth *et al.*, 2007; Vadeboncouer *et al.*, 2011) and spawning habitat (Lawson *et al.*, 2011) for aquatic organisms, such as fishes (Vander Zanden *et al.*, 2011; Gaeta *et al*, 2014). The three most common forms of littoral zone habitat structures are cobble, coarse woody habitat (CWH, often referred to as large woody debris), and aquatic vegetation. Structure found in littoral zones will be hereafter referred to as 'littoral structure'. Cobble (64-256mm, Wentworth, 1922) armors shorelines and provides interstitial spaces, which can be critical for fish refuge spawning (Beauchamp *et al.*, 1994; Glassic & Gaeta, 2019). In forested areas, littoral zones in close proximity to the riparian area can receive terrestrial sources of carbon, such as CWH. CWH can also be delivered from upstream sources through debris flows. Fishes can use littoral CWH as critical cover from predator avoidance (Sass *et al.*, 2006b). Additionally, aquatic vegetation is often present in littoral zones, which provides substrate for algal and invertebrate development and autochthonous carbon resources for fishes (Crowder & Cooper, 1982). Littoral structure is important for many levels of lentic food webs, from nutrient and sediment retention to macroinvertebrate production to fish persistence. However, the impact of lake level decline on littoral structure availability is severely understudied.

Only a few recent studies have highlighted the effects of multiyear drought on littoral structure loss and aquatic organisms. For example, multiyear drought cycles and the associated lake level decline was shown to reduce littoral cobble structure by > 96% in a large, deep, desert lake in Southwestern United States (U.S.), leaving cobble exposed along shorelines (Glassic & Gaeta, 2019). In this study, cobble acted as critical spawning habitat necessary for an endemic species of concern to complete their life cycle. Similarly, researchers studying a small inland lake in the upper Midwestern U.S. determined that multiyear drought driven lake level decline of just over a meter would leave CWH stranded along shorelines, degrading fisheries and nearly extirpating a fish population (Gaeta *et al.*, 2014). Multiyear drought has also been shown to leave aquatic vegetation in a shallow lake in Utah desiccating along the shoreline, decreasing macroinvertebrate population biomass and richness, which is critical prey for an endangered desert fish (Dillingham *et al., in prep*). Indeed, the health of biota in lentic ecosystems across the globe likely rely upon structure littoral zones provide. By expanding our understanding of littoral structure availability, we can begin to identify spatial patterns of lentic ecosystem responses to lake level decline under drought conditions. Such broad-scale evaluation can improve our understanding of the vulnerability of littoral structure to multiyear drought driven lake level loss and identify potential areas of concern. Additionally, this research uncovers hypotheses to test in order to identify the mechanisms of littoral structure loss.

Drought is defined by the U.S. Drought Monitor (USDM) as, “a moisture deficit bad enough to have social, environmental, or economic effects” (USDM, 2019), and nearly 75% of states in the conterminous U.S. experienced drought in mid-2012, (Figure 2, NOAA, 2016). Opportunely, the National Lakes Assessment (NLA, USEPA, 2017) surveyed over 1,000 lakes and reservoirs in 2012 and documented physical characteristics such as littoral and shoreline habitat structures, as well as vertical lake level decline. This dataset represents one of the largest and most robust lentic ecosystem assessments to date. My research takes advantage of this spatially vast dataset and multiyear drought conditions across the nation in 2012 to test whether relationships among multiyear drought, lake level, and littoral structure is limited to the few case studies described above or is pervasive across the United States.

Here, I evaluate whether the vulnerability of littoral structures (cobble, CWH, and aquatic vegetation) is driven by the magnitude of lake level decline and how ecoregion, lake origin, or lake morphometric characteristics may influence these relationships. The consequences of littoral structure loss can have cascading implications for entire ecosystems, especially given the variety of structure type and complexity of abiotic and biotic interactions that littoral zones host. Learning to manage aquatic ecosystems in the face of climatic change is crucial to maintaining healthy lentic ecosystems into the future.

Methods

Lake Physical Habitat Data

I obtained data from the NLA database (USEPA, 2017). Lake assessment data were originally collected through collaborations between the Environmental Protection Agency (EPA) and regional agencies (state and tribal). The NLA is a subset of the National Aquatic Resource Surveys, which describes the current condition (physical, chemical, biological, and recreation) of lakes and reservoirs in the U.S. in five-year intervals (c. 2007).

From 389,005 lakes identified in the National Hydrography Database, the EPA determined 159,652 lakes met sampling criteria. Of these, 111,818 lakes were accessible to sampling, from which 1,038 lakes were randomly sampled. Sites sampled included natural lakes, natural lakes managed as reservoirs, and man-made reservoirs. Data and agency-published preliminary analyses can be found on the NLA website and in the final report (https://www.epa.gov/national-aquatic-resource-surveys/nla, and USEPA 2016, respectively). Field crews successfully sampled the physical habitat characteristics of 1,018 water bodies during the summer of 2012 (May 2 - September 27). Full methods may be found in the NLA Field and Lab Manuals (USEPA 2010 and USEPA 2012, respectively).

I focused on the physical habitat portion of the dataset, which includes measurements of littoral and riparian habitat structures as well as aspects of lake morphometry (not including lake bathymetry). The NLA field sampling efforts intended to quantify magnitude and variety of: submerged aquatic macrophytes, substrate, and fish cover in the littoral, as well as riparian substrate, shoreline angle, and distance of lake level to high water mark. Additionally, within each lake, up to 10 stations were identified equidistant around the lake perimeter where habitat characteristics were measured. The physical habitat data consists of measurements for 10,134 sampling stations across 1,018 lakes (569 natural lakes (55.9%) and 449 man-made reservoirs (44.1%)). Data and metadata are readily available and can be found on the NLA website (https://www.epa.gov/national-aquatic-resource-surveys/nla).

Habitat Structure Analysis

Physical habitat data were used to calculate the probability of littoral structure loss (cobble, CWH) or absence (aquatic vegetation) across the observed range of lake level decline during the NLA sampling period of 5/2/2012 through 9/27/2012. The distance between the 2012 lake level and the mean high-water mark at each site was assumed to represent littoral zones at full pool, and that due to lake level decline under drought conditions, any exposed structure present was no longer available to aquatic biota (Figure 1). Submerged littoral structures were categorized by major bottom substrate habitat type: "cobble" is comprised of cobble where the mean 50th percentile of bottom substrate diameter = 248.7 mm, "coarse woody habitat" is comprised of all bottom substrate woody snag structures acting as fish cover > 0.3m in diameter, and "aquatic vegetation" is comprised of all inundated macrophytes. Structures stranded along shorelines (i.e., above the water line but below full pool) were considered potential littoral structures given an increase in lake level to full pool. The littoral, exposed shoreline, and total proportions of structure (cobble and CWH, respectively) was estimated using the following equations:

Equation 1.

$$Prop_{lit} = FC_{lit} * (\frac{Littoral_{sub}}{Littoral_{sub}+Shoreline_{exp}})$$

$$Prop_{exp} = FC_{exp} * (\frac{Shoreline_{exp}}{Littoral_{sub}+Shoreline_{exp}})$$

$$Prop_{tot} = Prop_{lit} + Prop_{exp}$$

where, FC_{lit} = fractional cover of littoral structure, FC_{exp} = fractional cover of riparian structure (CWH) and shoreline structure (cobble), $Littoral_{sub}$ = magnitude of submerged littoral zone (measured length in meters), $Shoreline_{exp}$ = magnitude of exposed shoreline habitat (measured length in meters), $Prop_{lit}$ = proportion of littoral structure, $Prop_{exp}$ = proportion of riparian structure, $Prop_{tot}$ = total proportion of structure. Littoral structure was considered lost if the total proportion of cobble or CWH was greater than the current submerged proportion. Aquatic vegetation presence was calculated as a greater than zero submerged presence in littoral zones, as this structure type cannot be detected on exposed shoreline. Additionally, I used a mixed effect ANOVA (Analysis of Variance) to test whether vertical loss and exposed shoreline from sites that lost >0-meters of lake level, respectively, were significantly different across EPA level-1 ecoregions (Eqn. 2). Southern Semi-Arid Highlands (SSAH) ecoregion was removed from all ANOVA analyses due to low sample size.

Equation 2. Mixed effect ANOVA model

$$\hat{y}_j = \beta X + \varepsilon_j \qquad \textit{for } j = 1 \ldots n \textit{ lakes}$$

$$\beta_{0j} \sim N(\mu_{\beta_0}, \sigma^2_{\beta_0})$$

$$\varepsilon_j \sim N(0, \sigma^2_{\varepsilon})$$

Here, βX is a matrix of coefficients and variables where variables are EPA Level-1 ecoregions, and the random effect structure is centered around the intercept. β_{0j} is normally distributed with mean (μ) and variance (σ^2). The residual error term, ε, is normally distributed around zero with a variance of σ^2. For this analysis, the random effect is ecoregion.

Drought Severity

Drought severity data were retrieved from the U. S. Drought Monitor (USDM) website (http://droughtmonitor.unl.edu/). Data were downloaded by county and year to determine counties that experienced short term and multiyear drought (short term = at least three consecutive weeks of D2 (Severe Drought) 1/1/2012 - 9/15/2012, multiyear = at least 52 non-consecutive weeks of D2 drought 1/1/2011 - 9/15/2012). Definitions of drought severity indices and associated Palmer Drought Severity Index ranges are defined in Table 2. I used a mixed effect ANOVA to test whether vertical loss and exposed shoreline, respectively, were significantly different across drought severity indices as defined by Eq. 2. Here, βX is a matrix of coefficients and variables where variables are drought severities ("No Drought" sequentially through "Extreme Drought"), where the random effect structure is centered around the intercept. For this analysis, the random effect is ecoregion.

Random Forest Classification

A random forest classification (Bremain, 2001) was used to independently test whether lake morphometric characteristics (e.g., shoreline angle, maximum depth, shoreline morphometry, and elevation), water body type, ecoregion, and/or drought severity were meaningful predictors of cobble, CWH, and aquatic vegetation availability. Shoreline morphometry is defined as follows in Equation 3 (Wetzel, 1990). A high value of shoreline morphometry indicates complex shorelines, and conversely, a low value indicates simplicity. From hereafter, shoreline morphometry will be referred to as shoreline complexity.

Equation 3.

$$Shoreline\ Morphometry = \frac{P}{2 * \sqrt{\pi * SA}}$$

where P = Perimeter and SA = Surface Area

Variable importance plots were used to identify the best predictor variables of littoral structure cover and informed the fixed effect structure of logistic mixed effect models. Partial dependence plots were used to visualize predicted littoral structure vulnerability across important predictor variables.

Lake Morphometric Characteristics

Lake morphometric characteristics (shoreline angle, maximum depth, shoreline complexity, and elevation) were explored because of their widespread availability within the NLA database and due to their high importance in Random Forest Classification analyses within this study. Additionally, these characteristics represent diverse and important physical aspects of lentic ecosystems. Shoreline angle is a good indicator of the magnitude of littoral zones, maximum depth is a proxy for lake size, shoreline complexity indicates shoreline complexity, and elevation is important to include because it dictates fundamental structure availability. First, I used a mixed effect ANOVA to test whether lake morphometric characteristics (shoreline angle, shoreline complexity, maximum depth, and elevation) were statistically different between lake origin with a random effect of ecoregion, or among ecoregion with a random effect of lake origin, as defined in Eq. 2. Here, βX is a matrix of coefficients and variables where variables are EPA Level-1 ecoregions and lake origin (natural or man-made) where the random effect structure is centered around the intercept. For this analysis, the random effect is ecoregion and lake origin, respectively.

Second, a Constrained Correspondence Analysis (CCA) was used to test whether cobble, CWH, and/or aquatic vegetation were correlated with specific lake morphometric characteristics (shoreline angle, maximum depth, shoreline complexity, and elevation). Third, a Principal Components Analysis (PCA) was used to test whether data within-lake morphometric variables (shoreline angle, maximum depth, shoreline complexity, and elevation) were correlated within ecoregion or lake origin (man-made or natural), respectively. Analyses were performed in RStudio statistical package using the ‘lme4’, ‘multcomp’, ‘multcompView’, and ‘vegan’ packages (version 1.1-20, 1.4-10, 0.1-7, and 2.5-4, respectively; R Development Core Team, 2019).

Mixed Effect Model Analysis

I used a hierarchical logistic mixed effect model to test the probability of littoral structure proportional loss between littoral and riparian zones (cobble and CWH) and probability of littoral structure absence (aquatic vegetation) over the range of observed vertical lake elevation loss. A hypothesis-driven approach was used to determine the fixed effect structure, where the predictor variables of interest were vertical lake elevation loss as well as the lake morphometric variable that best predicted structure availability as shown by the random forest classification. The intercept-only models (Eq. 4) were compared with the final models (Eq. 5) for each structure type to determine how much variance was explained by adding vertical loss and lake morphometric characteristics (cobble and CWH: shoreline angle, aquatic vegetation: elevation) to the models.

Equation 4. Intercept-only model

$\Pr(\hat{y}_{j[i]} = 1) = logit^{-1}\,(\beta_{0[i]} + \varepsilon_i)$ *for i = 1…n observations*

$\beta_0 \sim N(\mu_{\beta_0}, \sigma^2_{\beta_0})$ *for j = 1…n lakes*

$\varepsilon_i \sim N(0, \sigma^2_{\varepsilon})$

Equation 5. Final model

$\Pr(\hat{y}_i = 1) = logit^{-1}\,(\beta_{0[i]} + \beta_{1j[i]}x_{1i} + \beta_{2j[i]}x_{2i} + \varepsilon_{ij})$ *for i = 1…n observations*

$\beta_0 \sim N(\mu_{\beta_0}, \sigma^2_{\beta_0})$ *for j = 1…n lakes*

$\varepsilon_{ij} \sim N(0, \sigma^2_{\varepsilon})$

Here, $\hat{y}_{j[i]}$ is the is the probability of detecting habitat loss (cobble CWH, or aquatic vegetation) at each station sampled j, β_0 is the model random intercept of lake. β_1 is the slope term and estimated effect of vertical lake elevation loss on habitat loss, β_2 is the slope term and estimated effect of shoreline angle and elevation on habitat loss (cobble and CWH, and aquatic vegetation, respectively). β_0 is normally distributed with mean (μ) and variance (σ^2) of the respective β. The residual error term, ε, is normally distributed centered around zero, with unique variance (σ^2). Analyses were performed using RStudio, using packages 'lme4' (version 1.1-20) and 'arm' (version 1.10-1) (Bates *et al.*, 2015). Mixed effects modeling following procedures outlined in Gelman and Hill (2008) and Zuur *et al.*, (2009).

Results

Vertical lake level decline and exposed shoreline

Many lakes in the U.S. experienced a reduction in lake level at the time of the 2012 NLA survey (> 0m = 359, > 0.5m = 230, > 1.0m = 165, total n = 754). All EPA level-1 ecoregions located in the U.S. showed evidence of lake level decline and resultant exposed shoreline. However, the magnitude of mean vertical lake level loss and exposed shoreline (from >0m vertical loss) varied widely among ecoregions (vertical loss: 0.47m – 2.78m, exposed shoreline: 1.65m – 15.47, Figure 3). Consequently, a mixed effect ANOVA suggested significant differences in vertical loss and exposed shoreline among ecoregions (Figure 3). Further, I observed a pattern of increasing vertical loss in geographic area ranging from east to west (Figure 3a); however, this geographical pattern was less explicit for exposed shoreline (Figure 3b).

Drought Severity

Drought severity played a role in governing the degree to which lakes lost lake level and exposed shoreline (Figure 4). Vertical loss increased as drought severity increased; mean vertical loss increased sequentially from 0.94m – 1.41m (Figure 4a). Lakes that experienced ND (No Drought), D0 (Abnormally Dry), and D1 (Moderate Drought) did not differ significantly in vertical loss; however, a marked and statistically significant step-change in lake response to drought was apparent in lakes that experienced D2 (Severe Drought) and D3 (Extreme Drought) drought conditions. Exposed shoreline increased as drought severity increased through D2; mean exposed shoreline ranged from 4.11m – 8.78m, however lakes in D3 exhibited a lower value of exposed shoreline than in D2 (D2 = 8.78m, D3 = 6.43m, Figure 4b). Here, we see a separate phase shift where lakes that experienced low to moderate degrees of drought (ND, D0, and D1) exhibited between 4.11m – 4.84m of mean exposed shoreline. Lakes that experienced moderate to high degrees of drought (D2 and D3) exhibited around double the magnitude of exposed shoreline as low to moderate degrees of drought (D2 = 8.78m and D3 = 6.43m, respectively). Surprisingly, lakes that did not experience any degree drought (ND) experienced a non-zero amount of mean lake level decline (0.94m) and mean exposed shoreline (4.11m). Drought severity index D4 (Exceptional Drought) was removed from this analysis due to low sample size.

The magnitude of lake level decline varied across the nation in spatially inexplicit ways (Figure 5). Fundamental lake response to drought conditions was not dictated by ecoregion, instead rather importantly by shoreline slope, representing a disproportionate relationship between lake level loss and exposed shoreline. Unsurprisingly, an identical amount of lake level decline did not result in the same magnitude of resulting exposed shoreline (historical littoral zone) losses across the U.S. (Figure 6).

Random Forest Classification

Each random forest classification identified specific morphometric variables (e.g., shoreline angle, maximum depth, shoreline complexity, elevation, ecoregion, lake origin, and drought severity) as important to predicting cobble, CWH, and aquatic vegetation presence in the littoral zone. The mean of squared residuals and percent variation explained for each model is as follows: cobble (0.64, 45.08%), CWH (0.11, 17.25%), and aquatic vegetation (0.66, 65.61%). Variable importance plots identified that shoreline angle was the best predictor for cobble and CWH availability, and that elevation was the best predictor for aquatic vegetation availability (Figures 7-9). Partial dependence plots demonstrate that at moderate shoreline angles, cobble cover increases and at high elevations, aquatic vegetation cover decreases (Figures 7-9). However, the CWH partial dependence plots should be considered with caution due to poor model fit (17.25% of variation explained).

Lake Morphometric Characteristics

Lake morphometric characteristics varied between lake origin and among ecoregions. I found shoreline angle, shoreline complexity, and elevation varied significantly between lake origin, after accounting for ecoregion (all $Pr(>|z|) < 0.01$), respectively); however maximum depth did not differ significantly between natural lakes and reservoirs ($Pr(>|z|) > 0.05$, Figure 10). Natural lakes tended to have gentle shoreline angles, low shoreline complexity, and high elevation. Conversely, reservoirs were associated with steep shoreline angles, high shoreline complexity, and low elevation. All individual lake morphometric characteristics (shoreline angle, maximum depth, shoreline complexity, and elevation) showed significant variation among ecoregions after accounting for lake origin. A pattern emerged through visual assessment that values of shoreline angle and maximum depth increased across a west to east ecoregion gradient. Western lakes tended to be dominated by steep shoreline angles and deep lakes, while eastern lakes tended to be dominated by gentle shoreline angles and shallow lakes. However, shoreline complexity was equally variable among all ecoregions (Figure 10).

Lake morphometric characteristic variable relatedness in the PCA explained 55.1% of variance in axis 1, and 21.6% of variance in axis 2 (Figure 11a). No significant ecoregion-level (EPA Level-1, EPA 2019) separation was observed among combined lake morphometric variables (elevation, shoreline angle, shoreline complexity, and maximum depth) across PCA Axis 1 and PCA Axis 2; some ecoregions exhibited different vector directions, though high overlap was apparent in variable relatedness. (Figure 11a). Therefore, I cannot conclude that certain ecoregions consist of lakes with similar combined morphometric characteristics. Between lake origin (man-made and natural, Figure 11b), sites indeed separated into perpendicular vectors. However, a high degree of overlap remained in the PCA output, suggesting that some differences may be discernable between combined lake morphometric characteristics, but not enough to distinctly characterize lakes with distinct morphometry.

The lake morphometric characteristics variable relatedness in the CCA explained 17.4% variance on CCA Axis 1, but only 2.5% on CCA Axis 2 (Figure 12). Therefore, differences in morphometric variables and their relative strength (length of arrow) should only be evaluated across Axis 1. The CCA suggests cobble availability was associated with sites having steep shoreline angles, large maximum depths, high shoreline complexity, and high elevation. To a lesser extent, CWH availability seems to be associated with low shoreline angles, but the degree to which the relationship holds is unknown. The CCA indicated aquatic vegetation presence is driven by low elevation sites and low shoreline complexity.

Mixed Effect Model

The overall outcomes of these models suggest that lake level decline is associated with littoral structure vulnerability. The probability of cobble structure loss increased as lake elevation declined, though the model suggested that the probability of proportional littoral structure loss at 0.5m lake level decline was 92% (Figure 13-15). The probability of CWH loss exhibited a similar pattern, although CWH declined with nearly any lake level reduction; the probability of proportional structure loss at 0.5m lake level decline was 99%. The final model suggests that aquatic vegetation had a higher threshold to loss as lake elevation declined. Inundated macrophytes potentially tracked declining water levels; at 0.5m lake level decline, the probability of aquatic vegetation absence is 82%. Coefficient estimates and final model results are described in detail in Tables 2-4.

Discussion

Littoral zones are vital sources of energy and carbon for lentic food webs (Vadeboncouer & Vander Zanden, 2002; Vander Zanden *et al.*, 2011), and littoral structures provide refuge, prey production, and reproductive habitat for aquatic organisms (Sass *et al.*, 2006b; Helmus & Sass 2008; Lawson *et al.*, 2011). Yet, I found that over one-third of lakes in the NLA survey experienced reduced lake level and, consequently, altered littoral zones, as the magnitude of lake level loss increased with drought severity. A 1m loss in lake level resulted in a 26.7m median horizontal shift in littoral zone. Studies of biological consequences from lake level decline are limited, though ecological and economic ramifications of lake level decline are starting to be better understood. For example, a mere 1.1m drought induced lake level decline in a small, Laurentian lake in Wisconsin resulted in a 76% reduction in CWH density available to fishes in the lake, triggering a near collapse of the forage fish at the expense of a popular sportfish (Gaeta et al., 2014). Alternatively, a 5m drought induced lake level decline in a large desert lake in Utah/Idaho, resulted in roughly 86% reduction in cobble habitat, severely decreasing the spawning area and recruitment of an endangered and endemic fish species (Glassic & Gaeta 2018). Therefore, the 230 NLA lakes that lost >0.5m and 165 NLA lakes that lost >1m of lake level decline could, and likely will, see severe and negative effects on littoral structure and any biota that rely upon them. Looking beyond mere lake level decline, I found nearly any loss in lake level resulted in reduced littoral structure, and the magnitude of littoral structure loss varied with lake morphometric characteristics, such as the angle of the shoreline.

Lake level response to drought severity is multidimensional; decreased lake level shifts littoral zones downslope, exposing once-submerged structure and introducing deeper habitats to the photic zone. Decreased water volume due to drought also increases salinity and the concentrations of nutrients (e.g., phosphorous, Schindler, 2009), depending on the lake morphometry. This phenomenon of shifting littoral zones will become ever more common as multiyear drought cycles are projected to increase in frequency and severity (Ficke *et al.*, 2007; Bates *et al.*, 2008; IPCC, 2018), especially as humans continue to withdraw water for irrigation or municipal uses. In particular, lakes with shallow shoreline angles are at greater risk of losing littoral structure with lake level decline, as this geometrical relationship between littoral structure loss and lake level decline is primarily a function of shoreline angle. However, I found littoral structure was left stranded even in cases of abnormally dry drought conditions (D0). Therefore, no matter the severity of drought, lakes across the nation are at risk of littoral structure loss.

Lake level response to drought conditions was not simply dictated by ecoregion (i.e., characteristics of similar geography and biota, or uniform amounts of solar radiation or soil moisture). Additionally, lakes lost lake level and experienced exposed shorelines despite the degree of drought severity they faced. However, lakes that experienced moderate to high drought severities exhibited marked increases in the magnitude of lake level loss and, consequently, exposed shoreline. This step-change pattern suggests that in general, lakes may tolerate low to moderate degrees of drought (D0-D1) and exceed a strong threshold of lake level response to drought at high drought severities (D2-D3). Perhaps the geographical pattern of increasing lake level loss across Eastern to Western U.S. is indicative of inherent lake morphometry in Western mountainous regions, especially since the magnitude of lake level loss depends on lake morphometry (e.g., size and shape). Future analyses may consider evaluating the role latitude may play in order to dive deeper into geomorphic constraints of lakes and reservoirs in the U.S. One of the most surprising results from this analysis revolved around lakes that did not experience any drought (ND) as these lakes also exhibited changes in lake morphometry through lake level decline and exposed shorelines.

The mechanisms driving high variation in lake level loss and exposed shoreline in lakes experiencing no drought conditions are unknown. One potential explanation of the pattern is the identification of “full pool” in the dataset (i.e., the historical high-water mark may not actually be the functional full pool level). The pattern could also be driven by human alteration of water flows. In some places water can be withdrawn from lakes and piped to areas in need of freshwater, as exemplified through the Central Arizona Water project, which transfers water from the Colorado River Basin to dry areas in

Southern Arizona (Hanemann 2002). Perhaps in major drought years, this strategy is more commonly used, causing local drought conditions to fail to explain lake response to drought accurately (Central Arizona Project, www.cap-az.com). Additionally, ecoregions encompass very large spatial areas, creating the potential for including many diverse lakes and reservoirs. Together, these phenomena may help explain the lack of lake response partitioning across ecoregion or drought severity. My findings provide evidence that lakes are incredibly unique and do not respond to drought conditions uniformly across space.

Lake morphometric characteristic differences between lakes and reservoirs followed known patterns of these types of systems. For example, reservoirs were classified by steep shoreline angles and high shoreline complexity, which is compatible with the geomorphology in canyon reservoirs where river channels are dammed and canyons become filled (Braatne *et al*., 2008, Hayes *et al*., 2017). The pattern of increasing shoreline angle and, to a lesser degree, maximum depth across a geographic gradient was particularly interesting. For example, cobble structures tended to be more available in large, steep lakes, suggesting availability may be limited in the Eastern U.S. However, availability of CWH and aquatic vegetation were not well described by lake morphometric characteristics. Simply put, some lake morphometric variables might traditionally be thought of as geographically confined, but this analysis shows that each lake has a unique morphometric fingerprint. Further research is necessary to understand the mechanisms driving littoral structure vulnerability to drought, perhaps focused on landscape position (lake position within a watershed) instead of elevation, land cover, or historic geomorphology (e.g., whether a lake was glaciated) to understand mechanisms driving littoral structure availability and vulnerability.

The National Lakes Assessment dataset is the largest lentic habitat assessment to date, is spatially extensive at the national scale, and provides a unique opportunity to study broad-scale patterns of fish habitat response to drought conditions. However, due to the scope of this assessment effort, several data limitations exist; most notably, habitat assessment was a visual survey (i.e., field crews did not perform snorkel or scuba surveys or hydroacoustic substrate mapping). Additionally, the dataset was temporally limited to the summer of 2012 and exhibited spatially coarse resolution at each individual lake. Moreover, the NLA survey assumed full pool represented non-drought conditions. Other critical uncertainties that cannot be determined from the available data include the rate of lake level decline, community structure of fishes, invertebrates, or aquatic macrophytes, delivery mechanisms of littoral structure, any biological consequences of altered littoral structure, and lake stratigraphy: the grain size available at depth or buried under fine sediment. These limitations and uncertainties that exist within the NLA are important to note; however, the spatial scope of this dataset remains unprecedented and provides a unique opportunity to study lake habitat on a national scale.

Cobble is a littoral structure important for bank stabilization and is crucial spawning habitat (Lane *et al.*, 1995; Ruzycki *et al.*, 1998). I found that very small decreases in lake level (0.5m) resulted in 100% probability that the proportion of cobble substrate in the current littoral zone was less than the proportion of cobble in past full-pool littoral zones, therefore indicating loss. Changes in lake elevation have the potential to change the spatial extent of near-shoreline cobble exposure. Fine sediment once positioned in an off-shore, less energetic environment (pelagic), can be located closer to the shoreline (littoral) as lake levels decline. Here, wave action can resuspend fine sediment, exposing the cobble substrate underneath. Therefore, cobble acts as a dynamic habitat with a spatial extent that changes with lake level. (Yalin, 1972). Random forest classification and constrained correspondence analyses both suggested cobble availability was associated with deep maximum depths and steep shoreline angles. These findings dovetail nicely with what we understand about scouring potential due to wave action; that is, the potential to expose cobble increases with an increase in shoreline angle (Van Weele, 1965), and lakes with steep shorelines generally tend to be large.

Coarse woody habitat is a critical littoral structure that supports nutrient retention (Schindler *et al.,* 1996), promotes benthic invertebrate production (Roth *et al.*, 2007), and provides prey fish refuge (Lawson *et al.,* 2011; Gaeta *et al.,* 2014). Conversely, the lack of structure leads to altered behavior and lower growth potential in fishes (Ahrenstoff *et al.,* 2009; Gaeta *et al.,* 2014). I found any magnitude in lake level loss resulted in a decline in CWH availability. CWH is a highly stationary littoral structure since availability and transport is limited to riparian or upstream inputs. Therefore intuitively, CWH is associated with the terrestrial-aquatic boundary. Consequently, CWH is lost with any movement of the littoral zone away from the established shoreline. Costs to lentic ecosystems from losing terrestrial resources as lakes become increasingly disconnected from riparian zones are numerous. For example, allochthonous carbon inputs can decrease in the form nutrients needed for fish growth (Weidel *et al.*, 2008), and future CWH used by fishes for prey refuge and growth (Sass *et al.,* 2006a; Sass *et al.,* 2006b; Gaeta *et al.,* 2014). Despite the known importance of CWH to lentic food webs, I found the presence of CWH in lakes was not explained by lake morphometric characteristics, suggesting that further research is necessary to identify lake origins or regions that may be more vulnerable to losing this critical littoral structure. Further research should explore whether riparian characteristics such as urban, crop, or forest cover are good predictors of CWH presence at full pool.

Inundated aquatic macrophytes are littoral structures that can decrease nutrient concentrations, improve water quality (Dhote, 2007), reduce wave energy (Peters & Lodge, 2009), as well as support macroinvertebrate communities (Engle, 1985; Crowder & Cooper 1982; Dillingham *et al., in prep*) and fish habitat (Werner *et al.,* 1977; Mittlebach, 1981, Cowx & Welcomme, 1998). I found that the probability of aquatic vegetation was less vulnerable to absence as lake level declined; a 2.5m lake level decline resulted in 50% probability of absence in submerged littoral zones. My CCA suggests aquatic vegetation availability was associated with low shoreline complexity and low elevations, which align well with our knowledge that shallow lake areas with high light penetration often have vegetation present. Aquatic vegetation communities are relatively non-stationary, especially during the time of seed dispersal (Gurnell *et al.,* 2006). Therefore, I hypothesize inundated macrophytes may be able to "track" lake levels and persist throughout drought conditions if in a reproductive stage. For example, macrophytes can successfully colonize streams over timescales of months to years (Biggs, 1996). Unfortunately, drought-tolerant invasive macrophyte species are known to rapidly colonize disturbed habitat (Bornette & Puijalon 2009; Coughlan *et al.,* 2018); further research should explore whether shifts in littoral zones associated with multiyear drought create niche space for aquatic macrophyte invasions.

I have demonstrated lake level and, consequently, littoral structures are highly vulnerable to multiyear drought conditions. The mechanisms and rates at which these littoral structures can reestablish under reduced lake level conditions is highly variable as aquatic macrophyte reestablishment may take weeks to years depending on community composition (Fleming *et al.,* 2011), cobble exposure likely on the order of years to decades (depending on wind, sedimentation rates, and whether cobble is present under fine sediments) (Oak, 1984), and CWH taking potentially decades to millennia (Guyette & Cole 1999; Roth *et al.,* 2007), depending on the delivery of structure input. Perhaps the most consequential aspect of littoral structure loss associated with multiyear drought conditions, and an area most in need of future research, is the capacity, or lack thereof, for aquatic biota to be resilient to habitat loss and, following drought reprieve, habitat recovery. For instance, recent research has shown that macroinvertebrate taxa with relatively short life cycles reappear in macrophytes relatively soon after macrophyte reestablishment following reprieve from drought (Dillingham *et al., in prep*). Conversely, fishes with relatively longer life cycles have been shown to have individual-behavioral resilience to CWH addition to a lake (Ahrenstoff *et al.,* 2009; Sass *et al.,* 2012), but exhibit no population-level response after four years of CWH addition (Sass *et al.,* 2012). This suggests that food webs may take years to decades to fully recover from littoral structure loss associated with a multiyear drought cycle. As drought cycles continue to increase in duration as projected under future climate change scenarios, biotic recovery may be protracted following littoral structure loss. The question remains as to whether drought reprieve will last long enough for biotic recovery to be successful.

The integrity of lentic food webs and energy pathways must be further evaluated when preparing to manage our future resources in an ever-increasing drought-prone world. Climate change in the form of multiyear drought will continue to cause many lakes to experience lake level decline. We understand littoral structures are lost with lake level decline, which has the potential to result in negative biological consequences. Therefore, we need more information to link lake level decline, and structure loss and recovery, to biological loss and recovery across ecoregions. As a result of more frequent and severe multiyear drought cycles under future climate change, lake level decline and human infrastructure will continue to increase and become ever more pervasive. As climate change continues to force novel environmental constraints upon the Earth's ecosystems, scientists and resource managers must prioritize preserving the critical role that littoral structures play as environmental benefits to lake health and biotic persistence.

Tables and Figures

Table 1. Definitions of United States Drought Monitor drought severity indices, D0-D4. Corresponding ranges of Palmer Drought Severity Index (PDSI) are included for familiarity.

Category	***Description***	***Ranges of Palmer Drought Severity Index (PDSI)***
D0	Abnormally Dry	-1.0 to -1.9
D1	Moderate Drought	-2.0 to -2.9
D2	Severe Drought	-3.0 to -3.9
D3	Extreme Drought	-4.0 to -4.9
D4	Exceptional Drought	-5.0 or less

Table 2. Logistic regression mixed effect model analysis results of the probability of cobble loss as a function of lake level decline with stations (n = 1,451) nestled within site (j; n = 266). Model structure is shown in Equations 1 and 2.

	Group	**Parameter**	**Intercept model variance**	**Full model variance**
Random effects	Site (intercept)	$\hat{\beta}_{0j}$	2.402	1.415
	Parameter	**Coefficient**	**Coefficient estimate**	**Standard error**
Fixed effects	Intercept	$\hat{\beta}_0$	1.9402	0.4090
	Vertical Lake Loss$_j$	$\hat{\beta}_1$	0.8728	0.1571
	Shoreline Angle$_j$	$\hat{\beta}_2$	0.4223	0.1799

Table 3. Logistic regression mixed effect model analysis results of the probability of coarse woody habitat (CWH) loss as a function of lake level decline with stations (n = 468) nestled within site (j; n = 75). Model structure is shown in Equations 1 and 2.

	Group	**Parameter**	**Intercept model variance**	**Full model variance**
Random effects	Site (intercept)	$\hat{\beta}_{0j}$	-	1.674e-19
	Parameter	**Coefficient**	**Coefficient estimate**	**Standard error**
Fixed effects	Intercept	$\hat{\beta}_0$	4.01376	1.11649
	Vertical Lake Loss_j	$\hat{\beta}_1$	0.55888	0.42241
	Shoreline Angle_j	$\hat{\beta}_2$	0.09088	0.52892

Table 4. Logistic regression mixed effect model analysis results of the probability of aquatic vegetation absence as a function of lake level decline and elevation with stations (n = 2,934) nestled within site (j; n = 367). Model structure is shown in Equations 1 and 2.

	Group	**Parameter**	**Intercept model variance**	**Full model variance**
Random effects	Site (intercept)	$\hat{\beta}_{0j}$	11.18	12.08
	Parameter	**Coefficient**	**Coefficient estimate**	**Standard error**
Fixed effects	Intercept	$\hat{\beta}_0$	4.4583	1.1227
	Vertical Lake Loss_j	$\hat{\beta}_1$	-1.0704	0.1587
	Elevation_j	$\hat{\beta}_2$	-0.6147	0.1745

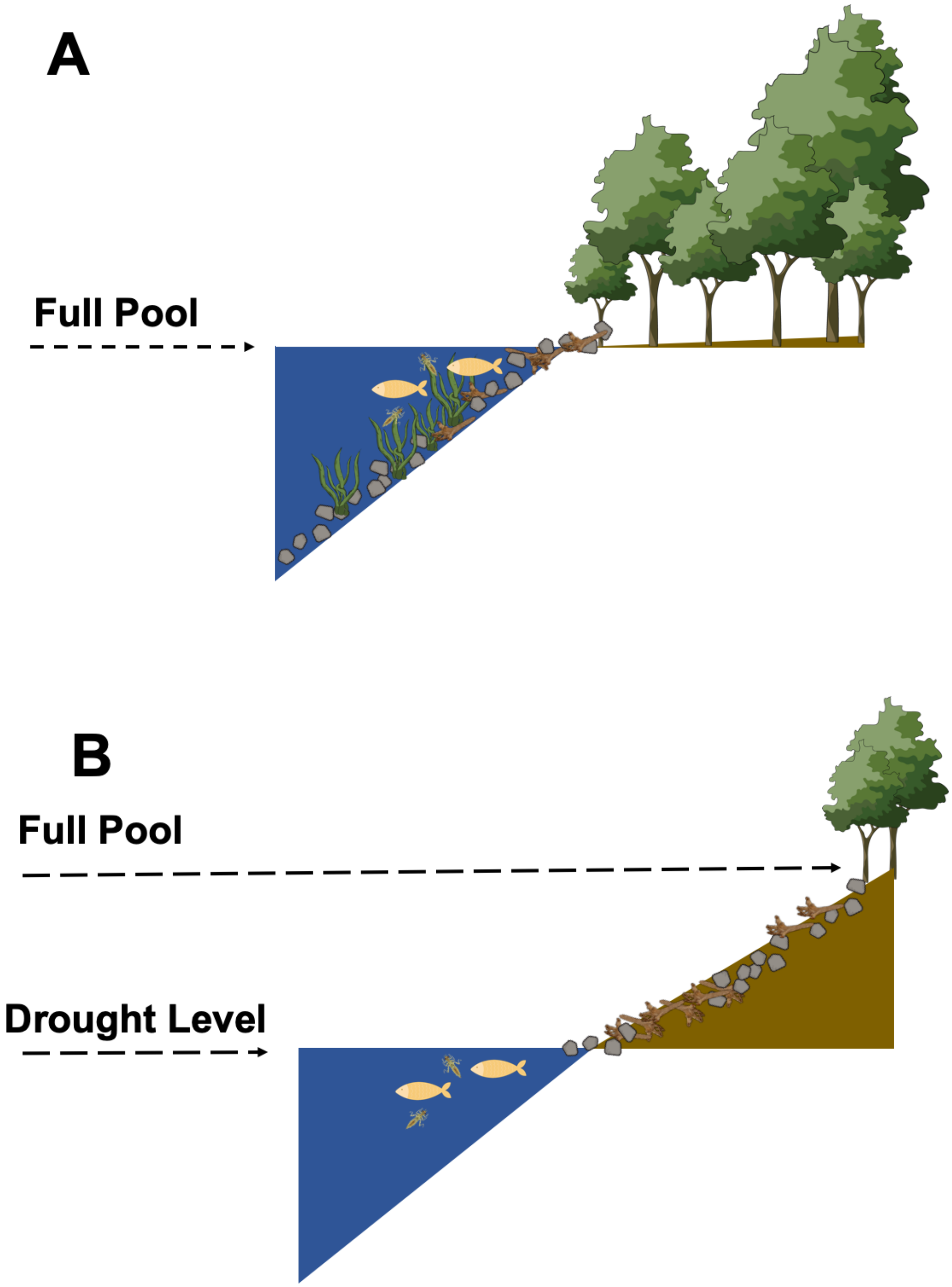

Figure 1. Conceptual model of lake level loss. A) Typical lake under full pool where littoral structure is submerged and the riparian zone is nearby full pool. B) Conceptual model of potential consequences of vertical lake elevation decline under drought conditions.

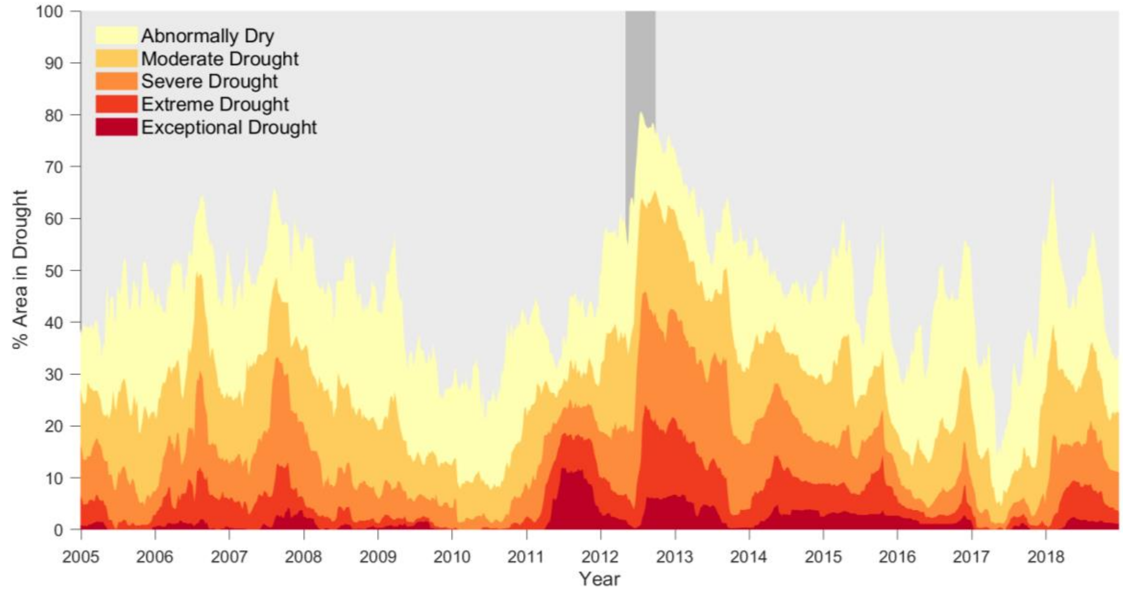

Figure 2. United States Drought Monitor depiction of elevated drought in 2012 compared to relative drought severity from 2005 through 2018. Drought severities range from D0 (Abnormally Dry) sequentially through D4 (Exceptional Drought). Gray bar represents the 2012 National Lakes Assessment sampling period.

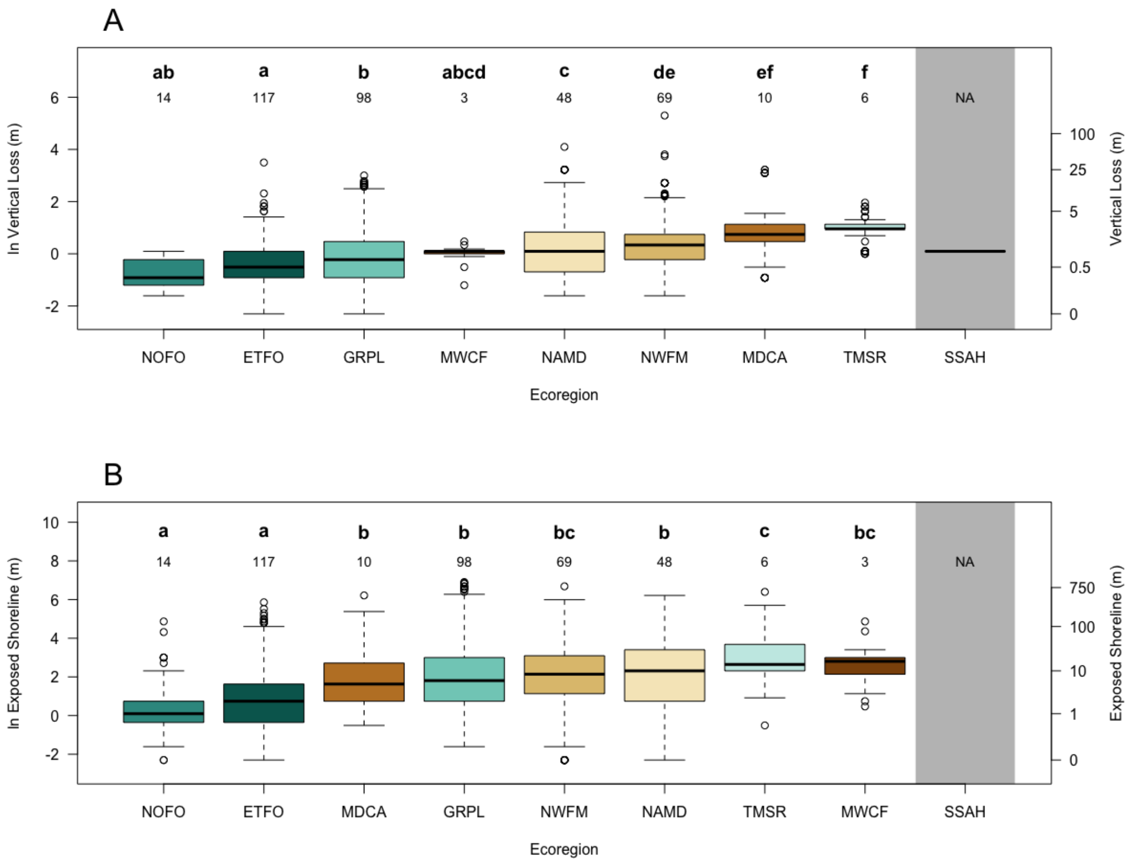

Figure 3. A) Range of vertical lake elevation decline among lakes across EPA Level-1 ecoregions with number of lakes sampled above each boxplot. B) Range of exposed shoreline among lakes across Ecoregions as documented by the National Lakes Assessment, 2012 of lakes that lost greater than 0-meter vertical loss. ETFO = Eastern Forest, GRPL = Great Plains, MDCA = Mediterranean California, MWCF = Marine West Coast Forests, NAMD = North American Desert, NOFO = Northern Forests, NWFM = Northwestern Forested Mountains, SSAH = Southern Semi-Arid Highlands, TMSR = Temperate Sierras. Singular letters a-f represent statistically significant differences while paired letters or repeat letters represent no statistical difference. Dark brown to deep teal color gradient represents ecoregions from west to east. SSAH was removed from analyses due to low sample size and is included for visual analysis on the far right (section in gray) in each ecoregion figure.

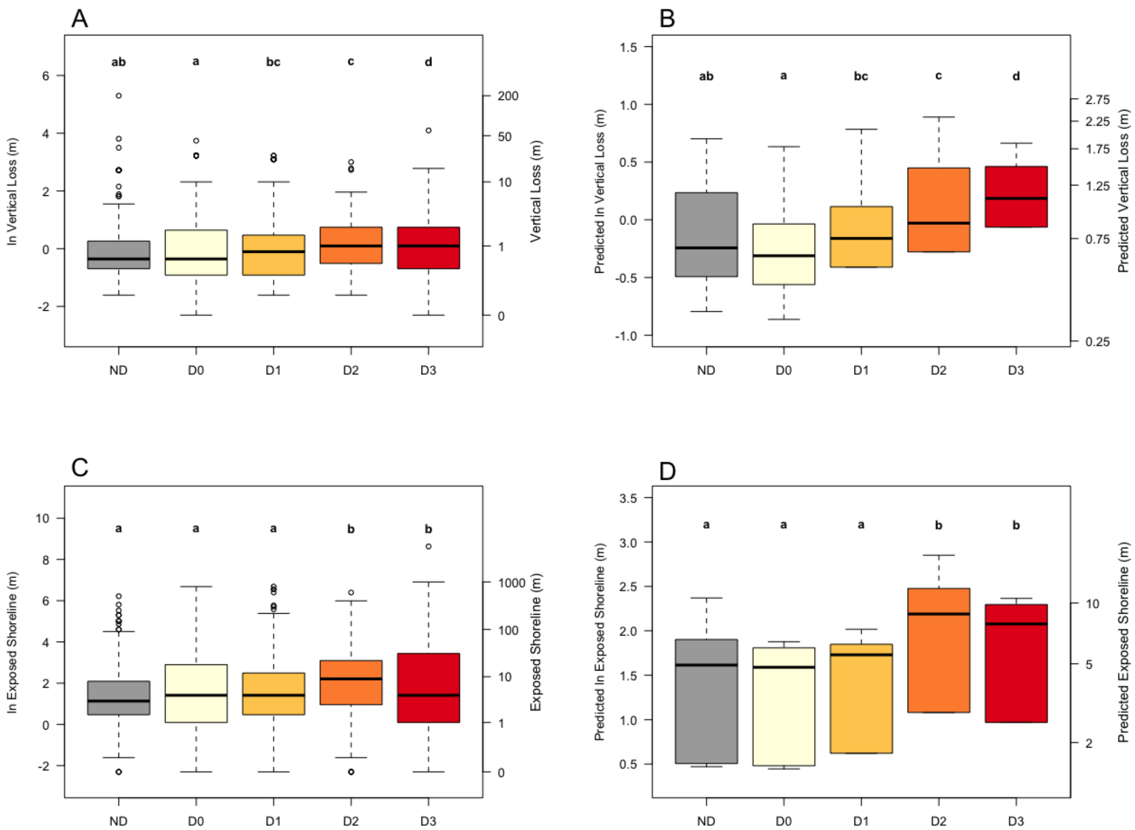

Figure 4. Range of, A) Vertical lake level loss (m), B) model predicted vertical loss, and C) Exposed Shoreline (m) and, D) model predicted exposed shoreline across U.S. Drought Monitor drought severity indices (ND-D3). ND = No Drought, D0 = Abnormally Dry, D1 = Moderate Drought, D2 = Severe Drought, D3 = Extreme Drought. Singular letters a-f represent statistically significant differences while paired letters or repeat letters represent no statistical difference.

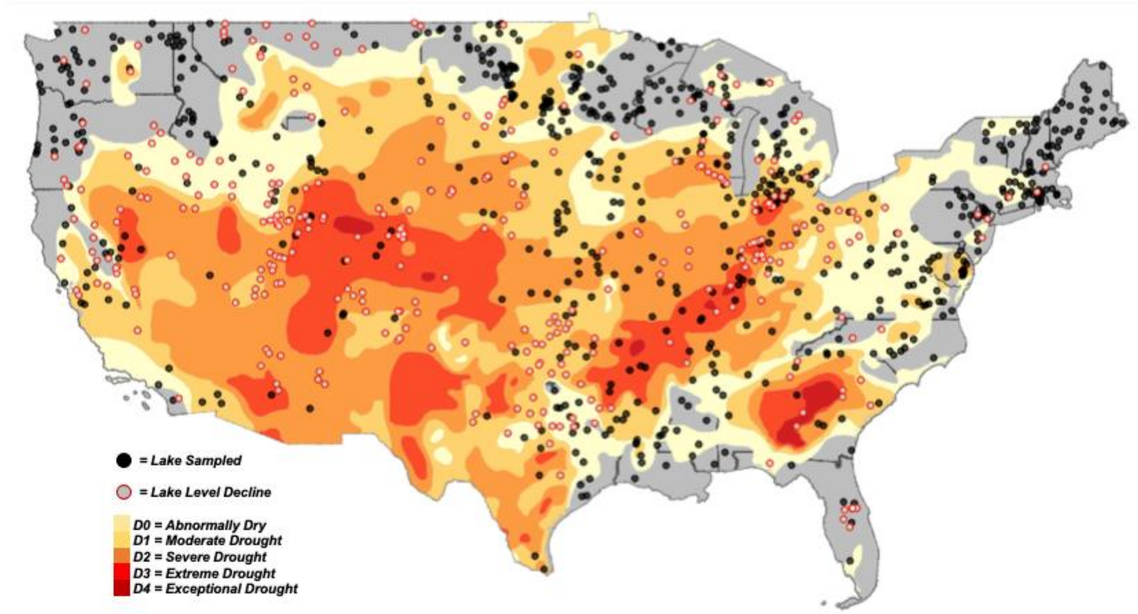

Figure 5. Map of the United States with a measure of drought severity from the U.S. Drought Monitor. Dark orange correlates with highest experienced drought, and light yellow represents low levels of drought. Sites sampled by the National Lakes Assessment in the U.S. in drought year 2012 are plotted as points, where red points represent lakes that experienced lake level decline.

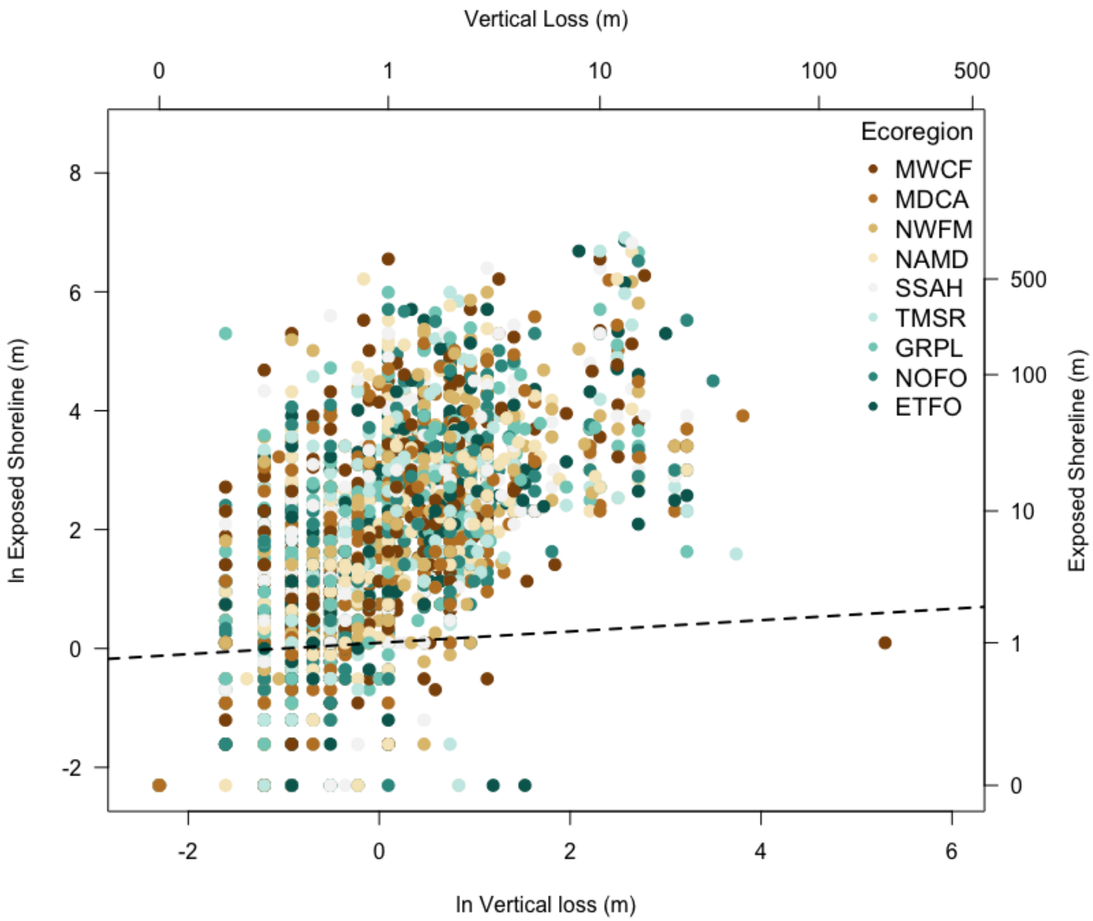

Figure 6. Lake level loss under drought conditions in meters and resulting exposed shoreline in log-log space. Points are colored by ecoregion and the line of identity (1 to 1 relationship) is overlain in black. NOFO = Northern Forest, NWFM = Northwestern Forested Mountain, ETFO = Eastern Temperate Forest, GRPL = Great Plains, NAMD = North American Desert, MDCA = Mediterranean California, SSAH = Southern Semi-Arid Highlands, TMSR = Temperate Sierra. Dark brown to deep teal color gradient represents ecoregions from west to east.

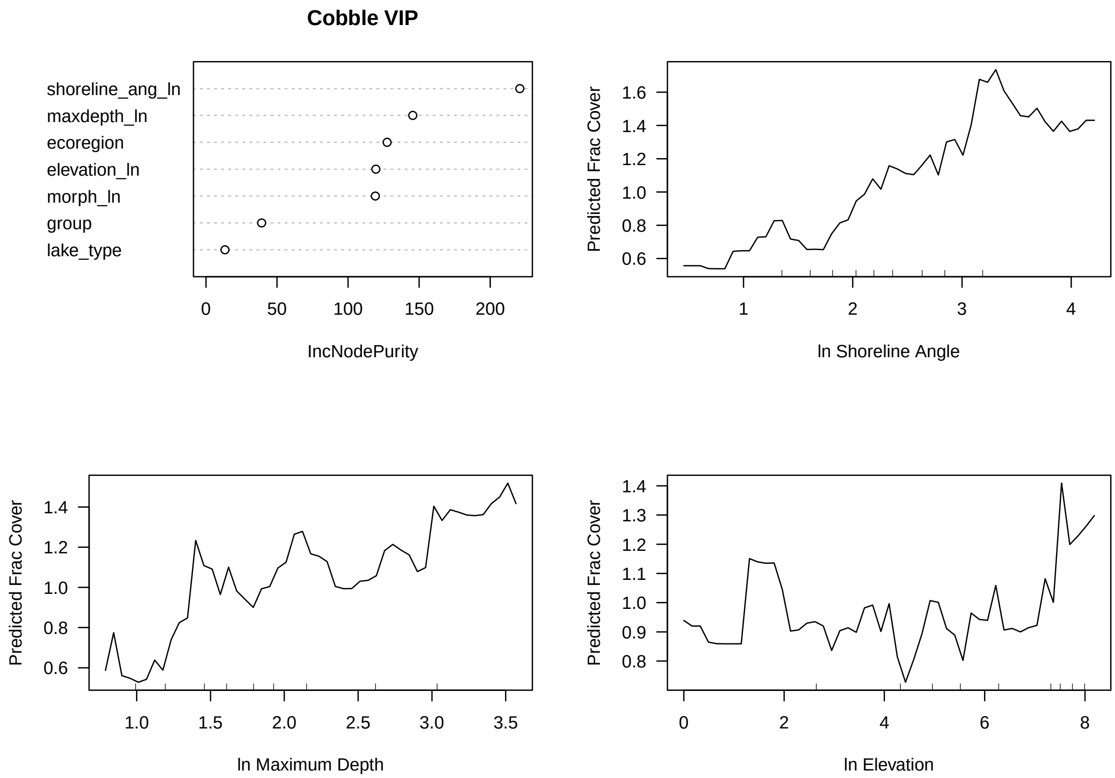

Figure 7. Random Forest Classification of Cobble as predicted by lake morphometric variables in panel A (shoreline angle, maximum depth, ecoregion, elevation, shoreline complexity, cluster, and lake origin). Shoreline angle is best predictor. Panels B-D are partial dependence plots for top three variables (shoreline angle, maximum depth, and elevation).

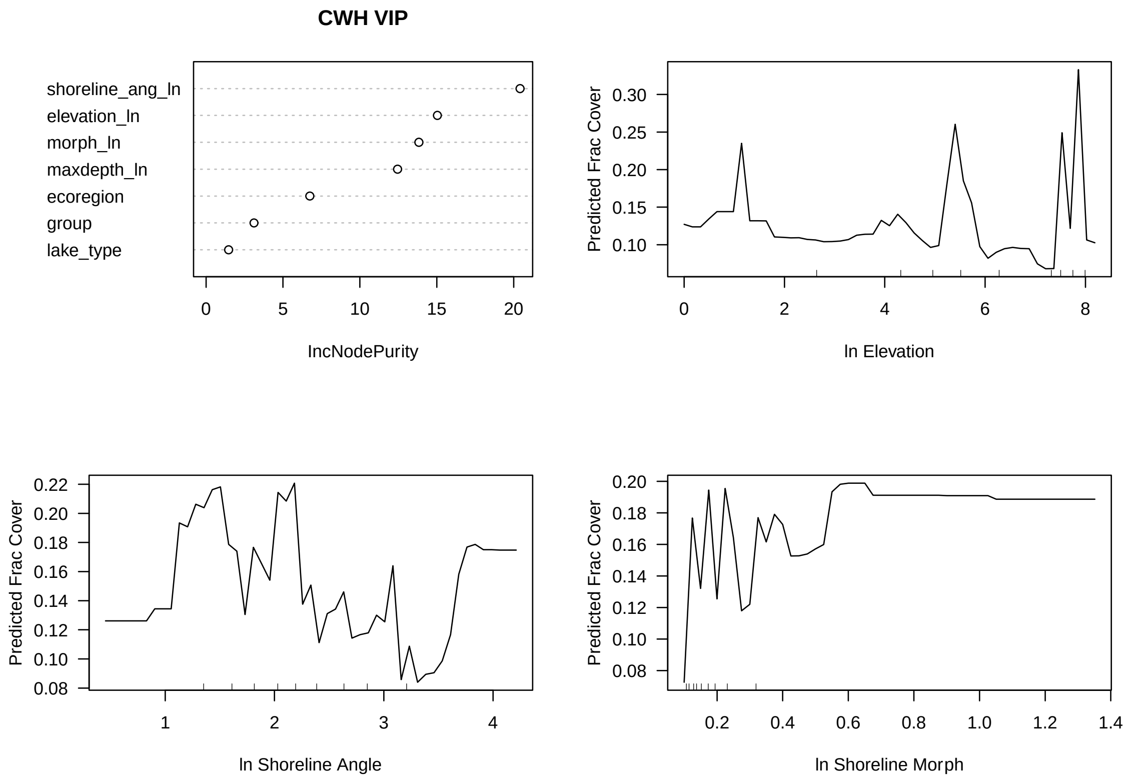

Figure 8. Random Forest Classification of Coarse woody habitat (CWH) as predicted by lake morphometric variables (shoreline angle, maximum depth, ecoregion, elevation, shoreline complexity, cluster, and lake origin). Shoreline angle is best predictor. Panels B-D are partial dependence plots for top three variables (shoreline angle, elevation, and shoreline complexity).

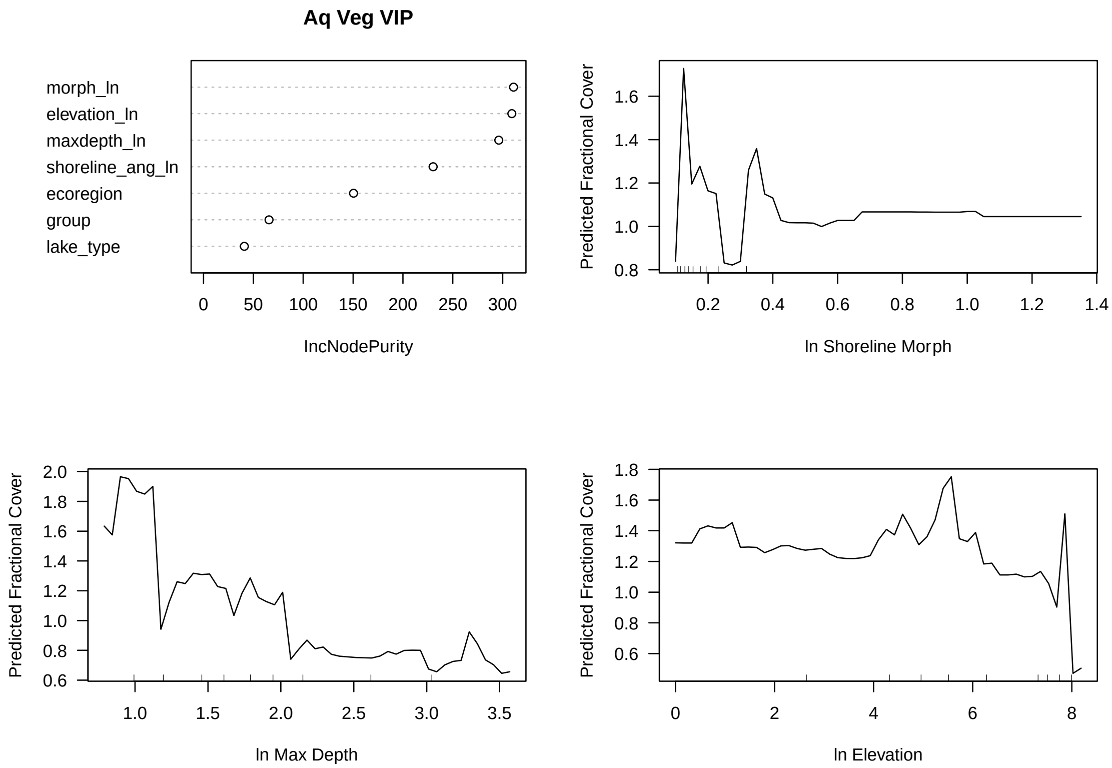

Figure 9. Random Forest Classification of Aquatic Vegetation as predicted by lake morphometric variables (shoreline angle, maximum depth, ecoregion, elevation, shoreline complexity, cluster, and lake origin). Shoreline angle is best predictor. Panels B-D are partial dependence plots for top three variables (shoreline complexity, elevation, and maximum depth).

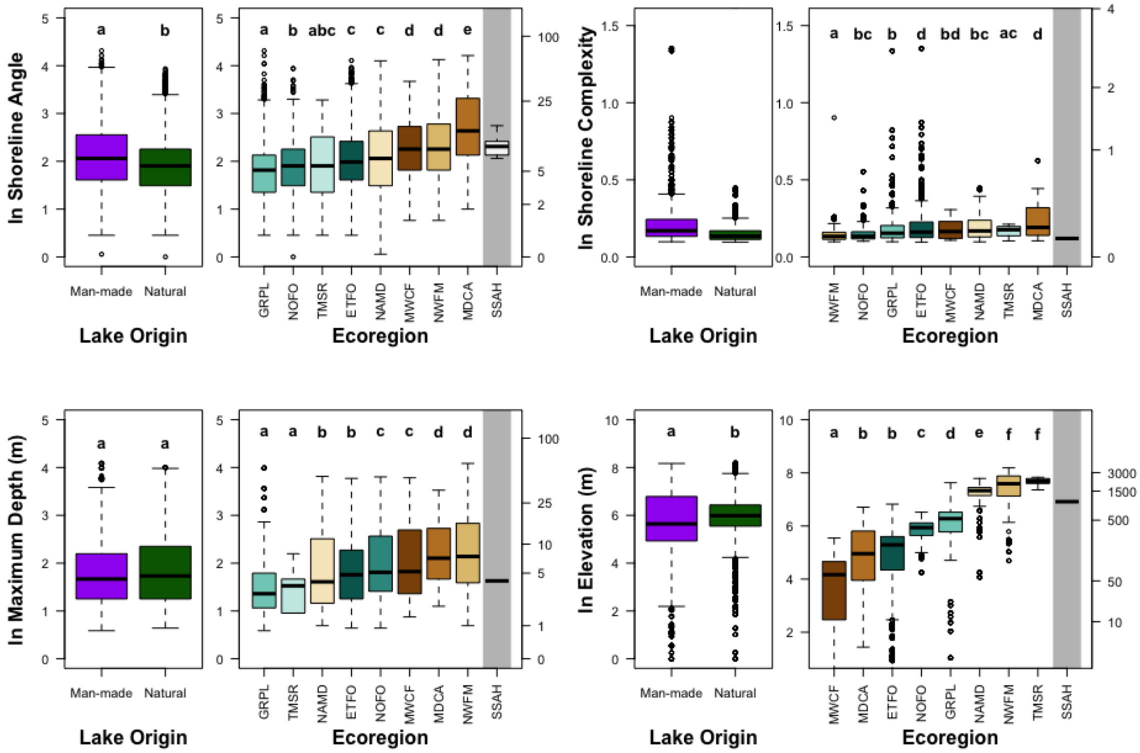

Figure 10. Lake morphometric characteristics values of: shoreline angle, shoreline complexity, maximum depth, and elevation plotted by lake origin (Man-made or Natural), and by ecoregion (ETFO = Eastern Temperate Forests, GRPL = Great Plains, MDCA = Mediterranean California, MWCF = Marine West Coast Forests, NAMD = North American Desert, NOFO = Northern Forests, NWFM = Northwestern Forested Mountains, SSAH = Southern Semi-Arid Highlands, TMSR = Temperate Sierras). Singular letters a-f represent statistically significant differences while paired letters or repeat letters represent no statistical difference. Dark brown to deep teal color gradient represents ecoregions from west to east. SSAH was removed from analyses due to low sample size and is included for visual analysis on the far right (section in gray) in each ecoregion figure.

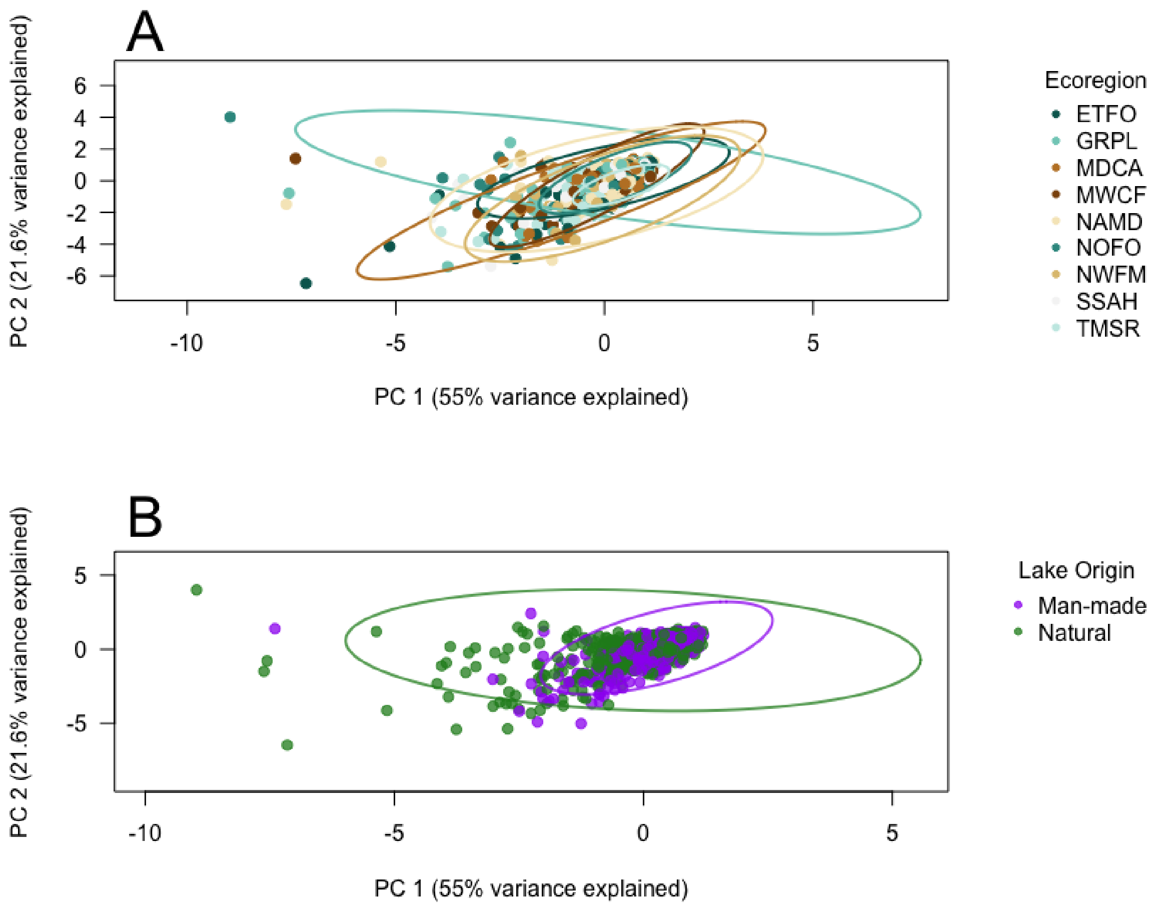

Figure 11. Principal Components Analysis of lake morphometric characteristics (shoreline angle, maximum depth, shoreline complexity, elevation) colored by A) Ecoregion (NOFO = Northern Forest, NWFM = Northwestern Forested Mountains, ETFO = Eastern Temperate Forests, GRPL = Great Plains, NAMD = North American Desert, MDCA = Mediterranean California, SSAH = Southern Semi-Arid Highlands, TMSR = Temperate Sierras). Brown to green color gradient represents ecoregions from west to east. B) Lake origin (man-made is labeled in purple, natural is labeled in green). The 99% confidence intervals for each ecoregion and lake origin are overlain. 55% of the variance is explained on the x-axis, and 21.6% of the variance is explained on the y-axis.

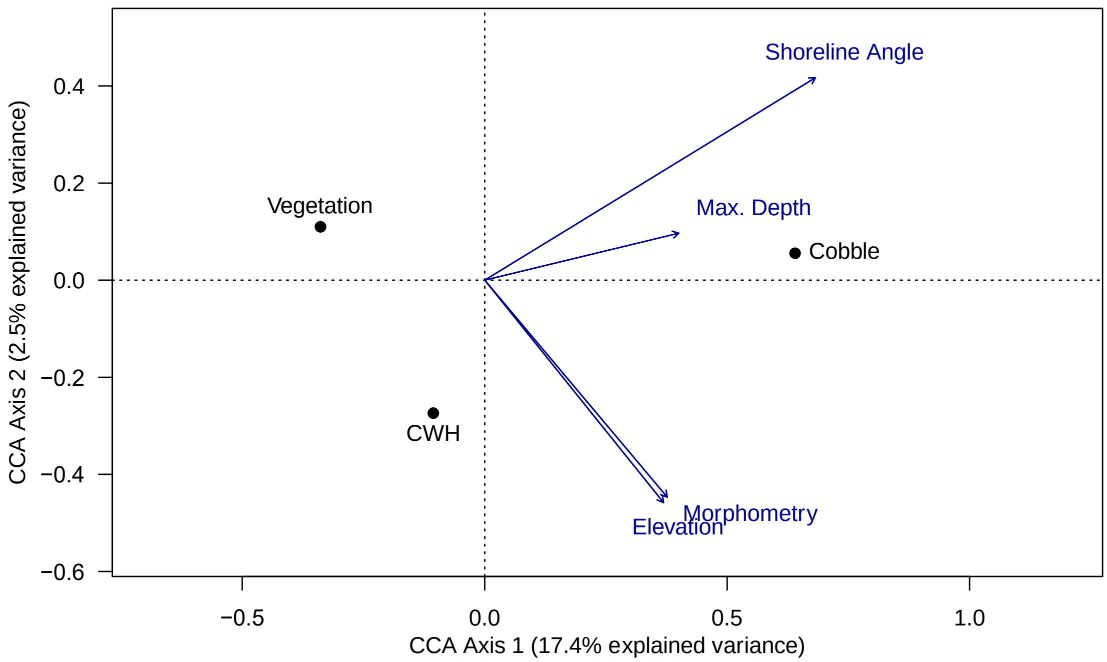

Figure 12. Constrained Correspondence Analysis of lake morphometric characteristics: shoreline angle, maximum depth, shoreline complexity (morphometry), and elevation. The blue vector length corresponds to variable strengths. Littoral structure (cobble, coarse woody habitat (CWH), and aquatic vegetation (vegetation)) availabilities are plotted in variable space. The x-axis explained 17.4% of the variance, and the y-axis explains 2.5% of the variance).

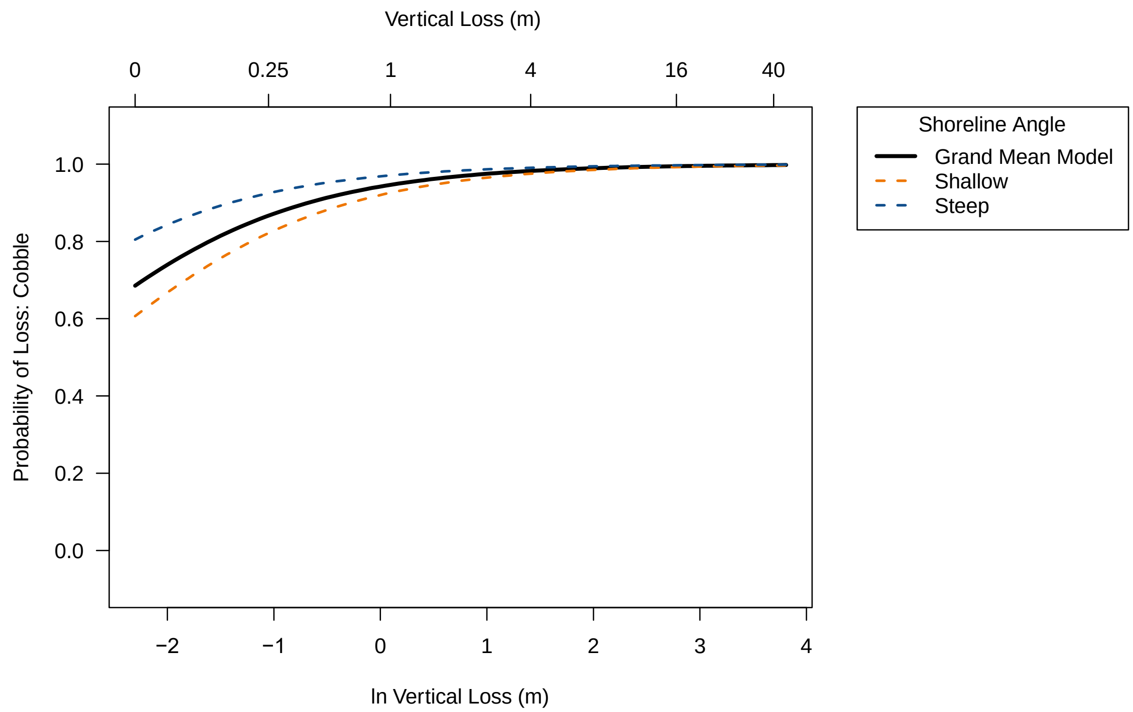

Figure 13. The probability of losing cobble under increasing vertical lake level. Shallow and steep shoreline angles (fixed effects, colored as yellow and blue) are overlain. The black line represents the grand mean model. Model coefficients are noted in Table 2.

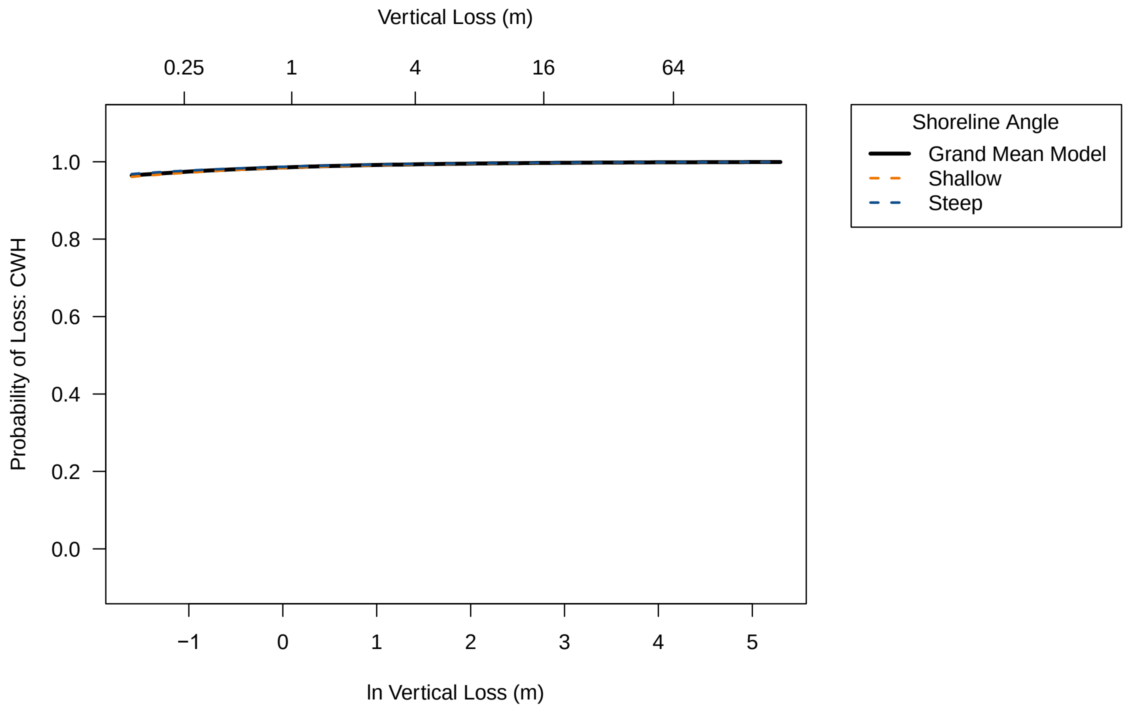

Figure 14. The probability of losing coarse woody habitat (CWH) under increasing vertical lake level. Shallow and steep shoreline angles (fixed effects, colored as yellow and blue) are overlain. The black line represents the grand mean model. Model coefficients are noted in Table 3.

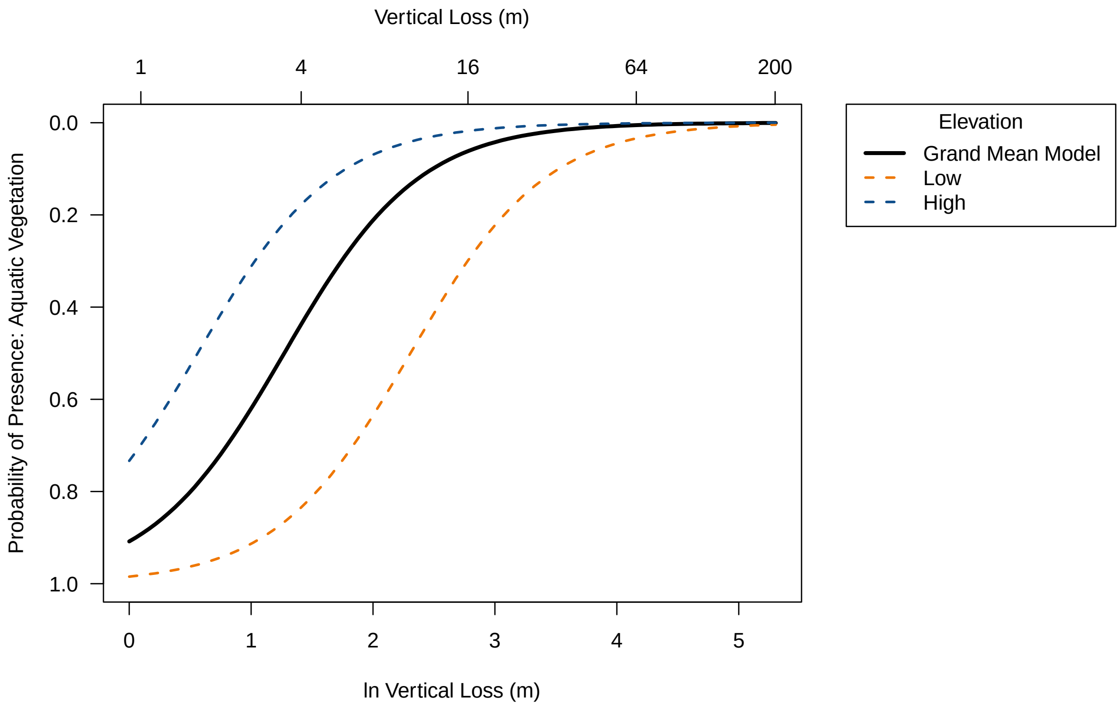

Figure 15. The probability aquatic vegetation absence under increasing vertical lake level. Low, and high elevation (fixed effects, colored as yellow and blue) are overlain. The black line represents the grand mean model. Model coefficients are noted in Table 4.

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APPENDIX

APPENDIX A

Cluster Analysis

I applied Ward Hierarchical Clustering to identify groups of lakes that were physically similar to each other by clustering lake morphometric variables (shoreline angle, elevation, shoreline complexity and maximum depth).

Five major clusters of distinct lake origins were identified within the cluster dendogram through visual analysis. Lake morphometric variable relatedness among physical lake features that potentially drive cluster groupings are shown in Fig 1A.

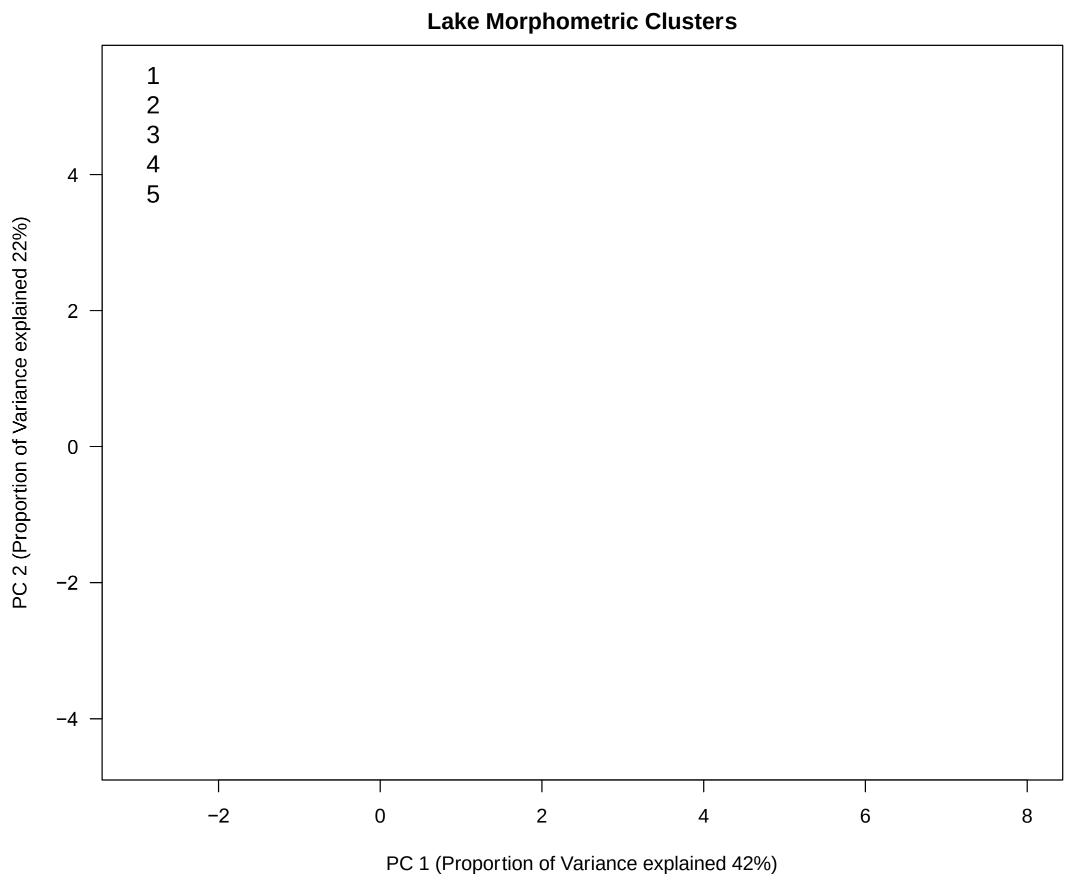

Figure 1A. Principal Components Analysis of lake morphometric characteristics (shoreline angle, maximum depth, shoreline complexity, and elevation) colored by clusters defined by Ward Hierarchical Clustering.