THESIS

ASSESSING VEGETATION REESTABLISHMENT ON DISTURBED HIGH MOUNTAIN LAKESHORES FOLLOWING HISTORIC DAM REMOVAL IN ROCKY MOUNTAIN NATIONAL PARK, COLORADO, USA

Submitted by

Amy C. Goodrich

Department of Forest and Rangeland Stewardship

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Master's Committee:

Advisor: Mark Paschke
Co-advisor: Paul Meiman

David A. Steingraeber
Jayne Jonas-Bratten

ABSTRACT

ASSESSING VEGETATION REESTABLISHMENT ON DISTURBED HIGH MOUNTAIN LAKESHORES FOLLOWING HISTORIC DAM REMOVAL IN ROCKY MOUNTAIN NATIONAL PARK, COLORADO, USA

Dam removal has entered the public spotlight in recent years, due to growing safety, economic, and environmental concerns related to dams. Removal is increasingly seen as a way to address not only the risks associated with aging and/or obsolete dams, but also as a tool for ecological restoration.

In 1982, then-79-year-old Lawn Lake Dam in Rocky Mountain National Park failed, resulting in three deaths, and extensive monetary damages and destruction of natural resources within the Park. This was followed by a policy decision to remove three dams in the Park between 1988 and 1990, returning the former reservoirs to their previous natural lake water levels, and re-exposing nearly 13 hectares of scoured shoreline, completely denuded of vegetation by approximately 80 years of inundation. The disturbed lakeshore areas were left to undergo passive restoration. In the years immediately following dam removal, one short-term (3 year) revegetation study was conducted at Lawn Lake, and informal observational data were gathered by NPS personnel at a handful of plots established at the disturbed lakeshores of Bluebird, Sandbeach, and Pear Lakes. However, no further published analyses of data were made available, and until 2014 the vegetation at these lakeshores had not been surveyed to determine longer-term effects of damming and dam removal to reestablished vegetation.

The goal of this study was to identify any persisting effects of historic damming and subsequent dam removal on vegetation characteristics such as species richness and diversity and community composition in the previously submerged lake margin areas surrounding the formerly dammed lakes, as well as the more elevated surrounding areas that had not been inundated. To do this, in July to September of 2014 I conducted surveys of vascular plant cover by species in 150 plots at nine high mountain lakes, including the four formerly dammed lakes and five undammed reference lakes. Site-specific environmental variables slope, aspect, elevation, elevation above current waterline, and soil texture were recorded at each plot. Plots were categorized as "elevated" or "lake margin" based on an elevation cutoff from the current waterline, to separate plots that had been previously submerged at dammed lake sites from more elevated sites that had not. I analyzed data from plots in each category for the effect of lake type (formerly dammed or reference) by fitting linear mixed models to species richness and diversity response. I performed a hierarchical cluster analysis that identified eight distinct vegetation communities, and performed non-metric multi-dimensional scaling (NMS) to explore relationships between vegetation community composition and site-specific measured environmental variables.

No significant differences in vegetation characteristics of the elevated areas were found between formerly dammed and reference lakes. In previously submerged areas of formerly dammed lakes, however, species richness was significantly higher, compared to the similarly-located lake margin areas surrounding reference lakes (+3.361, χ^2=8.919, p-val=0.003). All eight identified vegetation communities occurred at both formerly dammed and reference lakes. Slope and elevation were the measured environmental variables most strongly correlated with NMS axes (cumulative r^2 values of 0.18 and 0.086), indicating that they are the most influential measured environmental variables in structuring plant communities at these study sites.

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1. INTRODUCTION

Dams significantly impact riparian ecosystems by altering the flow regimes of rivers, altering river channels, floodplains, and river-to-reservoir transformations, limiting the transport of sediments and nutrients, fragmenting the continuity of habitats and biotic communities, and changing species composition (Petts 1984, Macdonald et. Al 1992, Ligon et al. 1995, Ward and Stanford 1995, Nilsson and Berggren 2001, Poff and Zimmerman 2010). Failure of structurally-unsound dams can cause catastrophic damage to natural resources, as well as expensive damage to downstream human infrastructure (Evans et al. 2000, FEMA 2001, American Society of Civil Engineers 2010). Growing safety, economic, and environmental concerns have led to increased attention on dam removal in recent years, as it is increasingly seen as a way to address not only the risks associated with aging and/or obsolete dams (Doyle et al. 2003), but also as a tool for river restoration (Bednarek 2001, Marks 2007, Winter and Crain 2008).

The construction of new dams was widespread throughout the 20th century, impounding rivers around the world for reasons including flood control, agricultural water storage, generation of hydroelectricity, and the creation of water-based reservoir recreation opportunities (Bednarek 2001). The rate of dam construction in the United States soared between 1950 and 1979, reaching a peak between 1970 and 1979, when construction was completed on 19,768 new dams (USACE 2014). Though this rate has slowed domestically, new dam construction projects continue at high rates internationally.

According to the US Army Corps of Engineers' 2013 National Inventory of Dams, 87,359 dams currently exist in the US, of which 55% are 45 years old or older (USACE 2013, metadata update 2015). Sediment accumulation in reservoirs and structural deterioration of the dam itself limit the estimated operational life expectancy of many dams to 50 years (Palmieri et al. 2001, FEMA 2001). This represents a significant number of structures whose functional lifespans have been exceeded, or which will be nearing lifespan exceedance by 2020. To keep an aging dam viable beyond this lifespan requires maintenance for hazard mitigation that may not be economically feasible (Orr and Stanley 2006).

The intentional dismantling and removal of dams is a relatively new practice, but one that is likely to experience domestic growth necessitated by the aging state of American dams and the shifting ecological values driving future decisions about their fates. Literature examining the effects of dam removal is largely limited to analyses of low-elevation former reservoirs in areas of high human use, or the temporally-limited revegetation that occurs during temporary reservoir drawdowns or seasonally in the water level fluctuation zones of reservoirs (Stanley and Doyle 2003, Auble et al. 2006, Orr and Stanley 2006). Given the ubiquitous dispersion of aging dams across a wide spectrum of elevations and ecosystems in the U.S. (USACE 2013), there exists a need for expanded research on the ecological impacts of dam removal, carried out over a wide range of geographic settings and related ecosystems (Shafroth et al. 2002, Auble et. al 2006).

The history of Rocky Mountain National Park's (RMNP) water and infrastructure management, which includes the historic removal of four high-elevation dams, lends itself to expanding the nascent study of post-dam removal revegetation processes and outcomes. The four former reservoir sites that exist in RMNP present an opportunity to study natural lakeshore revegetation following dam removal after a period of over two decades, in an ecosystem that has not been previously examined through this lens. Analysis of data collected on existing vegetation at these lakeshores nearly 25 years post-dam removal provides a clearer understanding of the longer-term effects of damming, and can inform developing practices related to future dam removals in high mountain ecosystems. This research addressed the following questions:

1. *Did historic damming at high mountain lakes alter the species richness and diversity of vegetation present in the lake margin (previously-submerged) areas surrounding high-mountain lakes? (Due to direct disturbance by inundation at dammed lake sites, this study hypothesizes significant differences in these lake margin areas.)*

2. *Did historic damming at high mountain lakes alter the species richness and diversity of vegetation present in the more elevated areas surrounding high-mountain lakes (>5.966m above the current waterline)? (Due to lack of direct disturbance by inundation at dammed and reference lakes, this study does not hypothesize significant differences in these elevated areas[1]).*

3. *How do environmental variables such as elevation, elevation above current lake level, slope, aspect, and soil texture influence plant community composition near the high-mountain lakes included in this study?*

[1] Although no significant differences are expected in these areas, it is possible elevated areas at historically dammed lakes may show unforeseen legacy effects to vegetation due to their prolonged proximity to the raised waterline and undefined associated changes in water availability during the period of damming.

2. STUDY AREA

Rocky Mountain National Park is located in the north-central region of Colorado. The park encompasses 107,549 hectares, and is split by the Continental Divide. Data recorded at the Natural Resources Conservation Service's Bear Lake SNOTEL climate station, located in the Park at an elevation of 2,896 m on the east side of the Divide, show an average annual precipitation (1989-2015) of 87.5 cm, with most falling as snow. The average minimum temperature occurs in January (-5.9°C), and the average maximum temperature occurs in July (13.9°C) (Natural Resources Conservation Service, United States Department of Agriculture 2016). Elevations in the park range from 2,326 m at the Big Thompson River to 4,346 m on Longs Peak. All nine lake sites included in this study are located on the east side of the park, characterized by lower annual precipitation than on the west side of the Divide. Five are located in the Saint Vrain watershed, and four are located in the adjacent Big Thompson watershed (Figure 1).

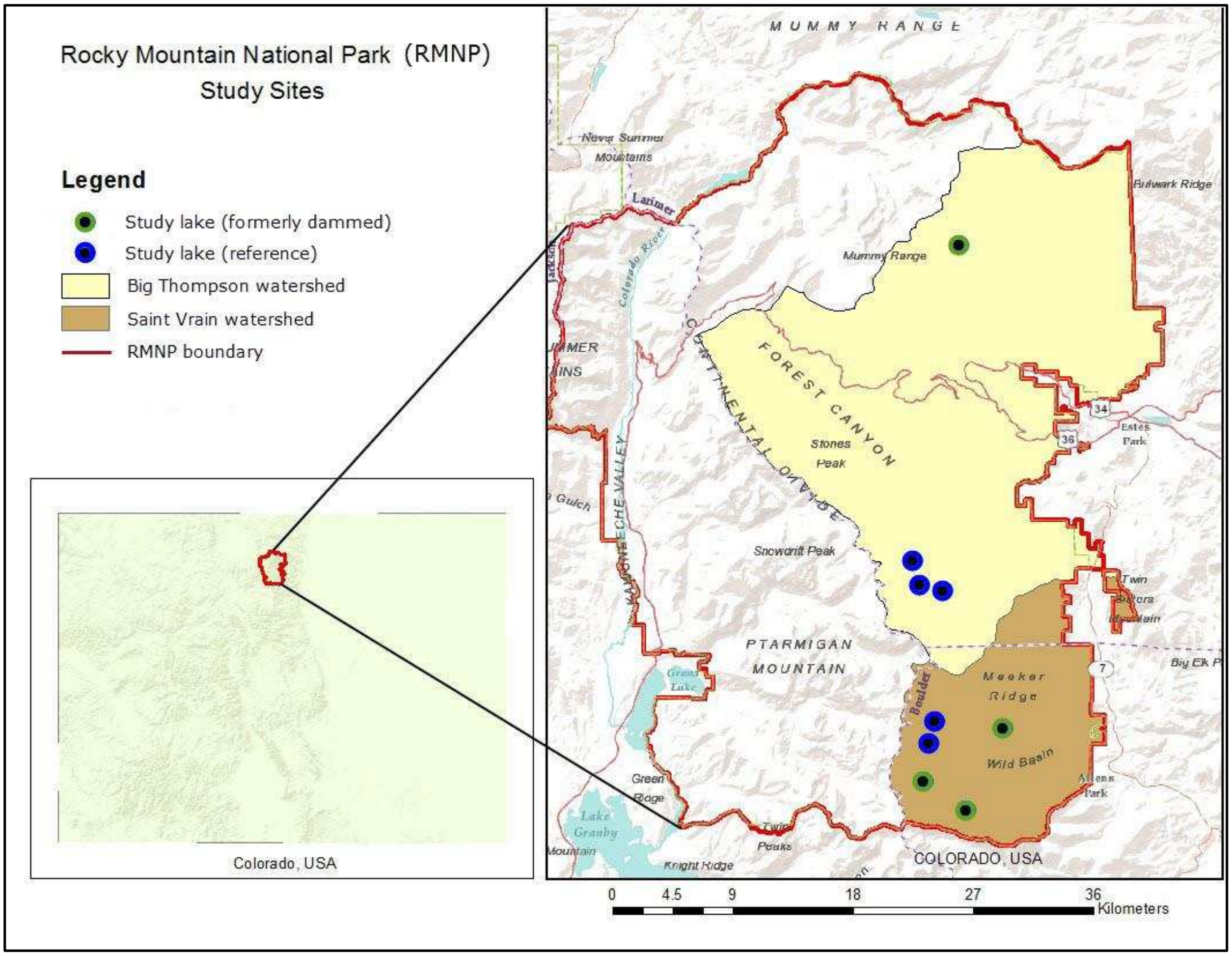

Figure 1. Map of sites included in study of lakeshore revegetation following dam removal, showing the locations of nine lake sites (four formerly dammed and five reference lakes) included in this study. All study lakes are located in the Big Thompson and Saint Vrain watersheds in Rocky Mountain National Park, Larimer and Boulder Counties, Colorado.

2.1 HISTORY

In 1982, Lawn Lake Dam in RMNP catastrophically failed, resulting in three deaths and over $72 million (2014 dollars) in damages, and unquantified destruction of natural resources in the Park (Karpowicz et. al 2010, Frank 2013). Spurred by this disaster, the National Park Service (NPS) and the Colorado State Engineer's office inspected the remaining dams in RMNP and concluded that existing dams at Bluebird Lake, Pear Lake, and Sandbeach Lake, owned by the

City of Longmont but located within park boundaries, were "*seriously deficient*," and classified them as "*Significant Hazard Potential*" dams. This, coupled with guidance from the National Park Service Safety of Dams (SOD) program stating that non-essential man-made structures within the National Park System should be deactivated and removed, drove the NPS policy decision to subsequently acquire the water rights and easements to all three remaining dams, and remove them between 1988 and 1990. All of these dams had been constructed to impede the outlets of existing natural lakes, raising their waterline levels for year-round increased water storage.

Along with breached Lawn Lake Dam, these three additional dam removals in RMNP lowered the waterlines at their four respective lake sites to pre-impoundment levels, re-exposing 12.89 hectares of scoured shoreline denuded of vegetation by approximately 80 years of inundation (Karpowicz et. al 2010). Resource managers at RMNP performed minimal vegetation salvage and relocation from the actual dam site at Lawn Lake to mitigate the extensive washout damage from this dam's failure, and also engaged in limited willow planting at the outlet of Pear Lake to minimize downstream increases in turbidity caused by sediment release associated with dam removal, for the protection of native greenback cutthroat trout habitat. Outside of the scope of these limited planting efforts, RMNP ecologists and managers determined that disturbed lakeshore areas should be allowed to undergo passive restoration via natural vegetation succession processes. One short-term (3-year, 1985-1987) study of initial vegetation colonization at Lawn Lake was conducted (Department of the Interior National Park Service 1993), and vegetation monitoring plots were informally established at Sandbeach and Bluebird Lakes, where data were collected intermittently by visiting Park personnel until 1997-1998, including photography and notes on observed species presence (Connor, personal communication). Meaningful data collection ceased after this time.

2.2 DAMS AND LAKE SITES

Lawn Lake Dam was an earthen dam constructed in approximately 1903 at the outlet of Lawn Lake, located at an elevation of approximately 3,353 meters. Bluebird Dam, the tallest dam of the four, was a concrete and rebar dam constructed between 1914 and 1923 at the outlet of Bluebird lake, located at an elevation of just under 3,348 meters. Sandbeach and Pear Lake Dams were earthen dams, also constructed between 1914 and 1923. They were located at the outlets of Sandbeach and Pear lakes, at approximate elevations of 3,136 and 3,227 meters, respectively. I identified five additional existent geographically-comparable high-mountain lakes using ArcGIS 10.1 (ESRI 2011, Redlands, CA). These are natural lakes with similar surface areas, existing within the same elevation band as the four formerly dammed lakes, within the Big Thompson and St. Vrain watersheds. This study included surveys at these five additional sites to provide reference data (Table 1).

Table 1**.** List of nine lakes with elevation (m) and locations (UTM) included in a study of lakeshore revegetation following dam removal in Rocky Mountain National Park, CO, USA.

LAKE	**ELEV (M)**	**UTM (WGS84)**
Bluebird L.	3347.74	444260.73mE 4449233.06mN
Eagle L.	3299.54	444573.2mE 4451411.21mN
L. Haiyaha	3116.78	443721.46mE 4461790.61mN
Lawn L.	3353.19	446543.22mE 4479805.55mN
Loch Vale	3105.88	444157.68mE 4460403.53mN
Mills L.	3029.8	445462.69mE 4460091.57mN
Pear L.	3227.12	446707.82mE 4447546.86mN
Sandbeach L.	3135.69	448839.58mE 4452275.97mN

3. METHODS

3.1 MAPPING

I assessed the terrain surrounding all nine lakes included in the study, up to a ground distance of 50 m from the current waterline using ArcGIS 10.1 (ESRI 2011, Redlands, CA). At the four formerly dammed lakes, I identified the boundary of the historic raised waterline using a combination of methods, including overlay comparison of recent 1:12,000 resolution aerial orthophoto imagery obtained from the National Agricultural Imagery Program (NAIP 2013) to ortho-rectified historic aerial imagery (USDA Forest Service 1946), where historic imagery was available, as well as elevation-based demarcation based on extant visual cues in current imagery, such as distinct soil, vegetation, or lichen coloration or texture pattern changes. This served to roughly stratify the four formerly dammed lake sites into two sampling categories: a lake margin zone immediately adjacent to the lakes, which at formerly dammed sites had been previously submerged (i.e., a ring of lower elevation terrain closest to the current waterline), and a second surrounding zone of more elevated terrain, which at formerly dammed lakes had not been submerged (i.e., a second concentric ring of terrain, more distant from the current waterline). This division into “lake margin” and “elevated” plot types is depicted in Figure 2.

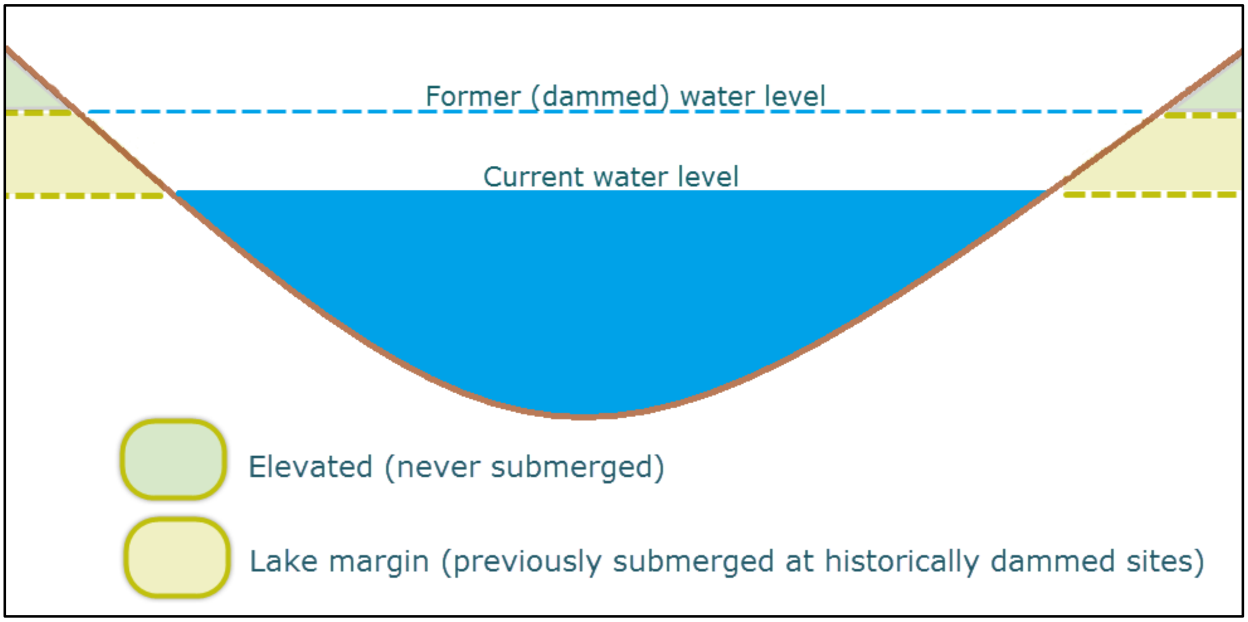

Figure 2. Cutaway depiction of lake included in post-dam removal revegetation study, with both the formerly-raised waterline during damming and the current, post-dam removal waterline shown. The related elevation-based distinction between lake margin (closer to the current waterline) and elevated (more distant from the current waterline) sampling categories is pictured.

I applied a second (independent) layer of stratification across the entire ground surface at all nine lake sites included in this study, using apparent floristic and hydrologic cues visible as differing coloration and/or patterning in recent aerial imagery to categorize sample areas surrounding the study lakes into one of five broad vegetation/plot types, based on visual characteristics: *majority bare soil/regolith*, *dry meadows*, *wet meadows*, *willow stands*, and *conifer stands*. While ground-truthing these classifications in the field several weeks prior to sampling, I concluded that the visual distinctions made between the "*bare soil/regolith*" and "*dry meadow*" vegetation community/plot type classifications using aerial imagery were not sufficiently distinct, likely due to the resolution of the imagery available, and so these strata were later combined (labeled "*sparse cover*") for the final sampling design. Finally, I used a stratifiedrandom point placement sampling design, enabling relevé sampling of representative stands in each of the remaining four distinct strata identified, at each lake site (Figure 3).

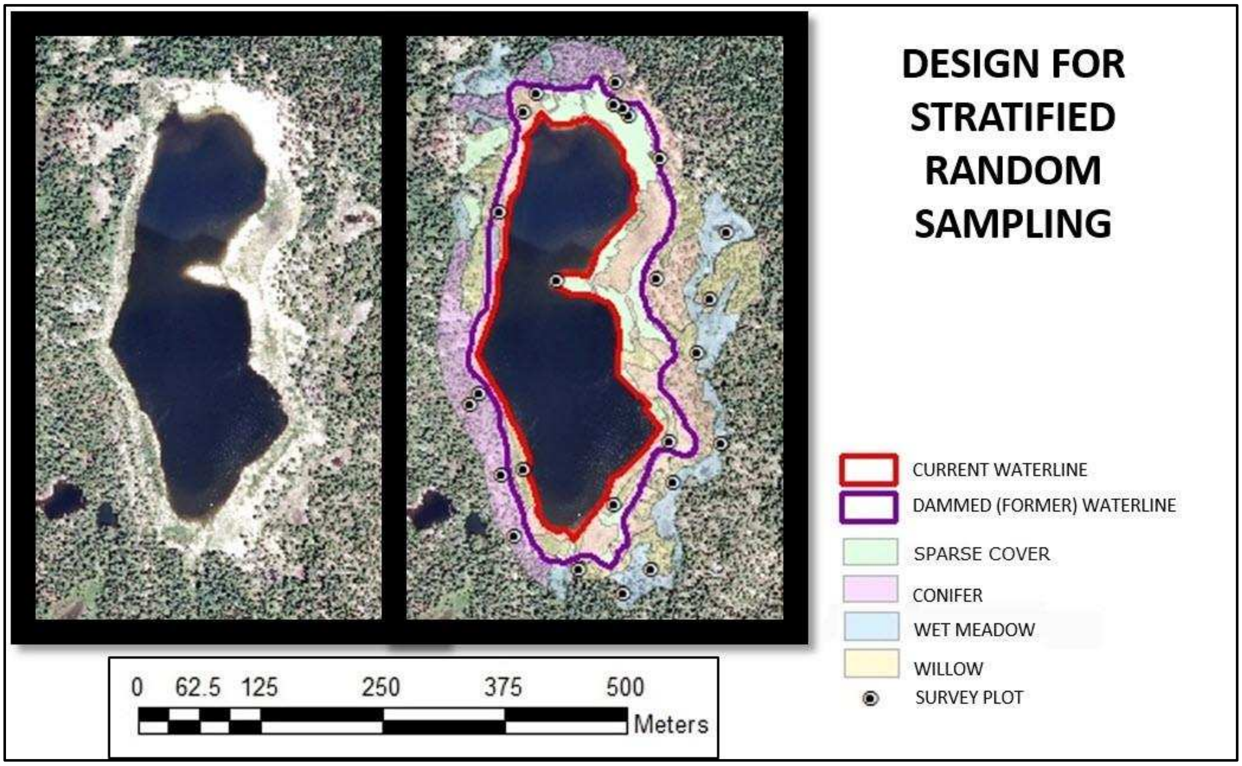

Figure 3. Aerial images of Sandbeach Lake, RMNP, CO, pictured to demonstrate sampling design stratification used in post-dam removal revegetation study. Left panel shows aerial imagery prior to delineation and addition of sampling stratification overlays made in Arc-GIS; right panel shows field map for sampling including added overlays of current and historic waterlines, plot type strata, and randomly-placed sampling point locations.

3.2 SAMPLING

Sampling was completed at N=150 of the point locations randomly generated, and occurred within all of the sampling vegetation/plot type classification strata present at each lake, although not all vegetation/plot type strata were present at each lake site (Table 2).

I navigated to sample points on the ground, when they were accessible; when terrain precluded safe navigation to a point it was omitted and the next accessible random point was used. I made ocular estimates of percent canopy cover for each vascular species present, combined percent cover of all non-vascular species (bryophytes and lichens), and percent surface water, rock, and bare soil cover within a 4-m^2 (2-m x 2-m) sample area. Nomenclature of the *Salix* genus follows The Genus Salix in North America North of Mexico (Dorn 2010); all other nomenclature follows Flora of Colorado (Ackerfield 2015). Soil particle size/type at each plot was visually assigned to one of three broad categories: coarse (rock, cobble, gravel, and sand >2 mm grain size); intermediate (medium to fine grain sand/silt/clay <2 mm grain size); or peat (predominantly organic accumulation), based on standards from USDA Textural Soil Classifications (USDA SCS 1987). Approximately 100 cm^3 of soil was collected from to a depth of 10 cm at 95 of the sample plots for analysis of percent organic matter by loss on ignition (Belyea and Warner 1996). However, soil could not be collected at all plots because total collected soil volume was limited by NPS research permit constraints. Aspect and percent slope were measured in each plot using a handheld clinometer and compass (aspect was later binned into nine categories for analysis: N, NE, E, SE, S, SW, W, NW, and flat). XYZ coordinates (northing/easting UTM coordinates, and elevation) at each plot were recorded using a Garmin eTrex Vista GPS unit; however, due to the limited accuracy of elevation measurements by handheld GPS units, more precise elevations at each plot's recorded XY coordinates was later obtained from a 10m-resolution digital elevation model (DEM) in Arc10.1 (ESRI 2011, Redlands, CA).

The average plot elevation above current waterline of all lake margin (i.e., previously submerged) plots sampled at the four formerly dammed lakes was 2.339 m (SD=1.814 m). Because elevational proximity to surface water and/or the water table is a key influential factor on plant community composition in montane riparian environments (Ramaley 1920, Körner

2003), an upper cutoff of $\bar{x}$+2SD (>5.966 m above current waterline) was used to assign plots at the remaining five reference lakes into comparable "lake margin" or "elevated" categories, for paired comparison with the lake margin and elevated plots surveyed at formerly dammed lakes.

Table 2. Summary counts of all plots surveyed in post-dam removal revegetation study in RMNP, CO. Plots counts are separated by specific lake, vegetation/plot type strata classification, and elevated|lake margin/previously submerged plot category.

LAKE	SPARSE COVER	WET MEADOW	WILLOW	CONIFER	TOTALS
*Eagle L.	0|8	0|3	0|3	0|3	17 (0|17)
*L. Haiyaha	0|4	0|2	0|0	0|6	12 (0|12)
*Loch Vale	0|4	0|5	0|0	0|2	11 (0|11)†
*Mills L.	0|1	0|6	2|3	2|3	17 (4|13)
*Thunder L.	1|2	0|4	0|3	4|0	14 (5|9)
Bluebird L.	2|5	0|3	1|3	2|1	17 (5|12)
Lawn L.	1|5	0|3	1|2	3|0	15 (5|10)
Pear L.	0|6	0|3	0|5	3|3	20 (3|17)
Sandbeach L.	0|5	1|2	1|4	1|5	19 (3|16)
TOTALS	**44 (4|40)**	**32 (1|31)**	**28 (5|23)**	**38 (15|23)**	**142 (25|117)**

*(Reference lakes, where there was no historic damming and therefore no inundation; plots within 5.966m elevation above the current waterline were categorized as "lake margin" for comparison to lake margin/previously-submerged plots at formerly-dammed lakes.)

†(Eight plots sampled on the same day at the Loch Vale lake site (2 sparse cover, 3 willow, and 3 conifer plots) were found upon data review to be lacking GPS coordinates recorded on-site. Because of this apparent equipment malfunction in the field, DEM plot elevations could not be obtained. These plots were omitted from elevation-based comparisons.)

3.3 STATISTICAL ANALYSIS

3.3.1 *Modeling species richness and diversity*

I used R version 0.99.486 (R Core Team 2015) and the RStudio interface (RStudio Team 2015) to fit linear mixed models with the *lme4* package (Bates et al., 2015) to explore species richness and species diversity[2] response variables. Separate analyses were conducted for elevated and lake margin plots (n=25 and n=117, respectively). I fitted linear mixed models of the relationships of lake type (formerly dammed or reference) to species richness and diversity. Model convergence was compared with a smaller-is-better fit criteria using Log Likelihood, Akaike Information Criterion (AIC), and Schwarz's Bayesian Information Criterion (BIC) scores (formula: [-2logL + kp], where L is the likelihood function, p is the number of parameters in the model, and k is 2 for AIC and log(n) for BIC) to select between models. Because of the somewhat limited size of the entire data set, I was cautious against attempting to fit an overparameterized model that would not be properly supported by the data. The most parsimonious model fit included lake type and vegetation/plot type classification as fixed effects, and lake and aspect as random effects, with random intercepts (but not random slope) included. Interaction terms were not found to improve the model fit, and so were not included. P-values for the effect of lake type were obtained from likelihood ratio testing between the full model and an otherwise-identical null model without lake type (the effect in question).

3.3.2 *Vegetation community classification, ordination, and correlation to site-specific variables*

For analysis of vegetation community composition, I used hierarchical cluster analysis to classify plots into vegetation community types. I performed Non-metric Multidimensional Scaling (NMS) on both plot types (lake margin and elevated) combined to explore species composition as it relates to measured environmental variables at the plot level through

[2] Species diversity comparisons were made using the Shannon-Weiner Index, calculated as $(H') = -\Sigma(pi * ln(pi))$ for each plot, where *p* is the proportion (n/N) of individuals of one particular species found (n) divided by the total number of individuals found (N), *ln* is the natural log, Σ is the sum of the calculations, and *s* is the number of species. A separate Simpson Index (dominance index) was also calculated for each plot $(D = 1/(\Sigma pi^2)$, but was highly correlated to H' values (Pearson correlation=.9953) and so was not separately used for any analyses.

ordination, using PC-Ord 5.0 (McCune and Mefford 2006). Plots that were lacking a complete set of environmental data (n=8) were omitted[3] from these analyses, as were plots in which no vascular plant species were observed (n=5). Sixty-one species occurring in only one or two plots and representing a total cover of less than 3% were classified as infrequently observed species, and were also removed from these analyses to reduce noise in results. Data from 137 of 150 sample plots were included in cluster and NMS community analysis.

To classify plant community types present in study plots, I performed a two-way hierarchal cluster analysis, utilizing a relative Sørenson distance matrix with flexible beta linkage of -0.25. To avoid an overly strong influence by dominant species, I performed relativization by species maximum on percent cover values in compositional data. The selection of a final number of vegetation community types was somewhat ambiguous, as the percent variance explained as a function of the number of clusters did not reveal an obvious "elbow" point of curve at which to prune a cluster dendrogram. The basic rule of thumb ($k = \sqrt{\frac{n}{2}}$) for selecting the most appropriate number of clusters (McCune and Grace 2002) suggested eight; this cutoff of eight clusters was also a point of division at which Monte Carlo testing of the significance of observed maximum indicator species analysis (ISA) values in tests of differing pruning points ranging from 5 to 13 vegetation groupings yielded the lowest average p-value across species (Dufrene and Legendre 1997, McCune and Grace 2002). The final selection of eight community groups was made by selection of the number of groups that optimized the average p-value of all species' ISA values. These eight plant communities were then named for the two (or three) species most prominent in each community, based on their high indicator values, their high frequency or abundance within

[3] These eight plots were all sampled on the same day at the Loch Vale lake site, and upon data review, were found to be lacking GPS coordinates recorded on-site. Because of this apparent equipment malfunction in the field, DEM plot elevations could not be obtained.)

that specific community type, or both. I again used PC-ORD 5.0 to perform a Multi-Response Permutation Procedure (MRPP) using a Sørenson distance measure to obtain the chance-corrected average within-group distance for each group.

I used NMS to explore the effects of measured environmental variables on species composition, using a random starting point and a Sørenson (Bray-Curtis) distance matrix, and running each model for 50 runs of real data, with 200 iterations of the final solution. The final number of axes was chosen via both visual inspection of the NMS scree plot (Figure 5) and stress testing, selecting the final number of ordination axes that balanced greatest improvement in model fit with the lowest level of stress, with a threshold of -5 reduction in stress required to justify any increase in dimensionality (Peck 2010). A Monte Carlo test confirmed that the solution provided an improved explanation of vegetation variation than what would be expected from randomized data ($p=0.019$). Quantitative environmental variables correlated with ordination axes were plot elevation, elevation above current waterline, and slope. Categorical environmental variables of aspect and soil texture were also used to further visually explore the ordination. The explanatory value of environmental variables was assessed based on cumulative r^2 values from linear regressions with NMS axes (r^2 values were summed across all three axes for each variable individually) (McCune and Grace 2002).

4. RESULTS

4.1 GENERAL OVERVIEW

Seventy-nine plots were sampled at five reference lakes (however as previously mentioned, eight plots at one reference lake were later omitted from analysis due to lack of elevation data, thus the inability to classify as either elevated/lake margin), and 71 plots were sampled at the four lakes that were formerly dammed (N=142). Of 71 plots sampled at formerly dammed lakes, 55 were located below the former waterline and classified as lake margin, while 16 were located above the former waterline, and classified as elevated. Using the elevation cutoff of +5.966 m above current lake waterline outlined in sampling methods, 62 of the plots sampled at reference lakes were similarly classified as lake margin, while 9 were classified as elevated.

A total of 147 observed vascular plant species were identified[4], of which 86 occurred in three or more sample plots, and 75 occurred in four or more plots. Only three species were observed in plots at all nine lake sites in the study (*Abies lasiocarpa*, *Antennaria rosea*, and *Picea engelmannii*), though 16 species were observed at seven or more of the lakes (Table 3). A total of 74 different vascular plant species were observed at Pear Lake, 73 at Bluebird Lake, 61 at Lawn Lake, 53 at Mills Lake, 52 at Thunder Lake, 49 at Sandbeach Lake, 47 at Eagle Lake, 46 at Loch Vale, and 25 at Lake Haiyaha. The most frequently observed species were *Abies lasiocarpa* (present in 75 plots), *Picea englemannii* (present in 66 plots), *Salix planifolia* (present in 55 plots), and *Antennaria rosea* (present in 39 plots). Of 86 species not classified as

[4] Although the majority of plants observed were identified to the species level, it was not possible to distinguish some graminoids below the family (*Poaceae*) or genus level (*Carex* and *Juncus*) due to collection outside of peak morphological development. These were broadly categorized (i.e., *Poaceae* unknown, *Carex* unknown, *Juncus* unknown) for inclusion in species richness and diversity calculations, but were excluded from cluster analysis.

infrequent, five were observed only in elevated plots (*Arnica cordifolia*, *Eleocharis quinqueflora*, *Pedicularis racemosa*, *Viola adunca*, and *Viola palustris*), while six were observed only in lake margin plots (*Pinus contorta*, *Poa secunda*, *Salix drummondiana*, *Salix glauca*, *Salix lucida ssp. lasiandra*, and *Salix monticola*). A seventh species, *Salix geyeriana*, was also notable in that it was observed in only one elevated plot, but was present in ten lake margin plots.

Table 3. List of vascular plant species observed most frequently in survey plots from post-dam removal revegetation study in RMNP, CO. Table lists all species observed at seven or more of the nine lake sites included in the study.

SPECIES	NO. LAKES WHERE OBSERVED	ABSENT FROM
Abies lasiocarpa	9	N/A
Antennaria rosea	9	N/A
Picea engelmannii	9	N/A
Calamagrostis canadensis	8	Sandbeach L.
Erigeron peregrinus	8	Mills L.
Juncus drummondii	8	Loch Vale
Pedicularis groenlandia	8	Loch Vale
Penstemon whippleanus	8	L. Haiyaha
Polemonium pulcherrimum	8	Sandbeach L.
Salix planifolia	8	L. Haiyaha
Senecio triangularis	8	Pear L.
Vaccinium scoparium	8	Loch Vale
Caltha leptosepala	7	L. Haiyaha, Sandbeach L.
Luzula parviflora	7	Loch Vale, Mills L.
Trisetum spicatum	7	Mills L., Thunder L.
Vaccinium myrtillus	7	Bluebird L., Sandbeach L.

4.2 SPECIES RICHNESS AND DIVERSITY

4.2.1 *Assumptions testing*

Visual inspection of Q-Q plots of residuals generated with R did not indicate any obvious deviation from normal distribution in species richness or diversity data. Three outlier plots were identified (Shannon diversity scores >2 standard deviations above the mean) but were not removed from the models, as they were all found at formerly dammed lakes, represented some of the highest richness counts in the study, and their Shannon diversity scores were not significantly outside the standard 2SD cutoff for normality ($\bar{x}$+2SD=2.508; Shannon diversity scores from these three plots were 2.534, 2.577, and 2.599). Levene's tests for homogeneity of variance indicated that the assumption of homoscedasticity was met by species richness and diversity data. These species richness and diversity data are further summarized in Table 4, and are shown in comparison boxplots in Figure 4.

Table 4. Mean, variance, and standard error of species richness and diversity data collected in post-dam removal revegetation study in RMNP, CO. Calculations were made separately for elevated and lake margin/previously submerged plot categories, grouped by lake type (formerly dammed or reference).

ELEVATED PLOTS						
	DAMMED			**REFERENCE**		
	Mean ± se	Min	Max	Mean ± se	Min	Max
RICHNESS	9.437 ± 1.218	3	18	8.222 ± 0.983	5	14
DIVERSITY	1.398 ± 0.148	0.422	2.197	1.559 ± 0.123	1.137	2.155

LAKE MARGIN PLOTS						
	DAMMED			**REFERENCE**		
	Mean ± se	Min	Max	Mean ± se	Min	Max
RICHNESS	9.137 ± 0.618	0	21	6.29 ± 0.446	0	15
DIVERSITY	1.488 ± 0.083	0	2.41	1.158 ± 0.07	0	1.524

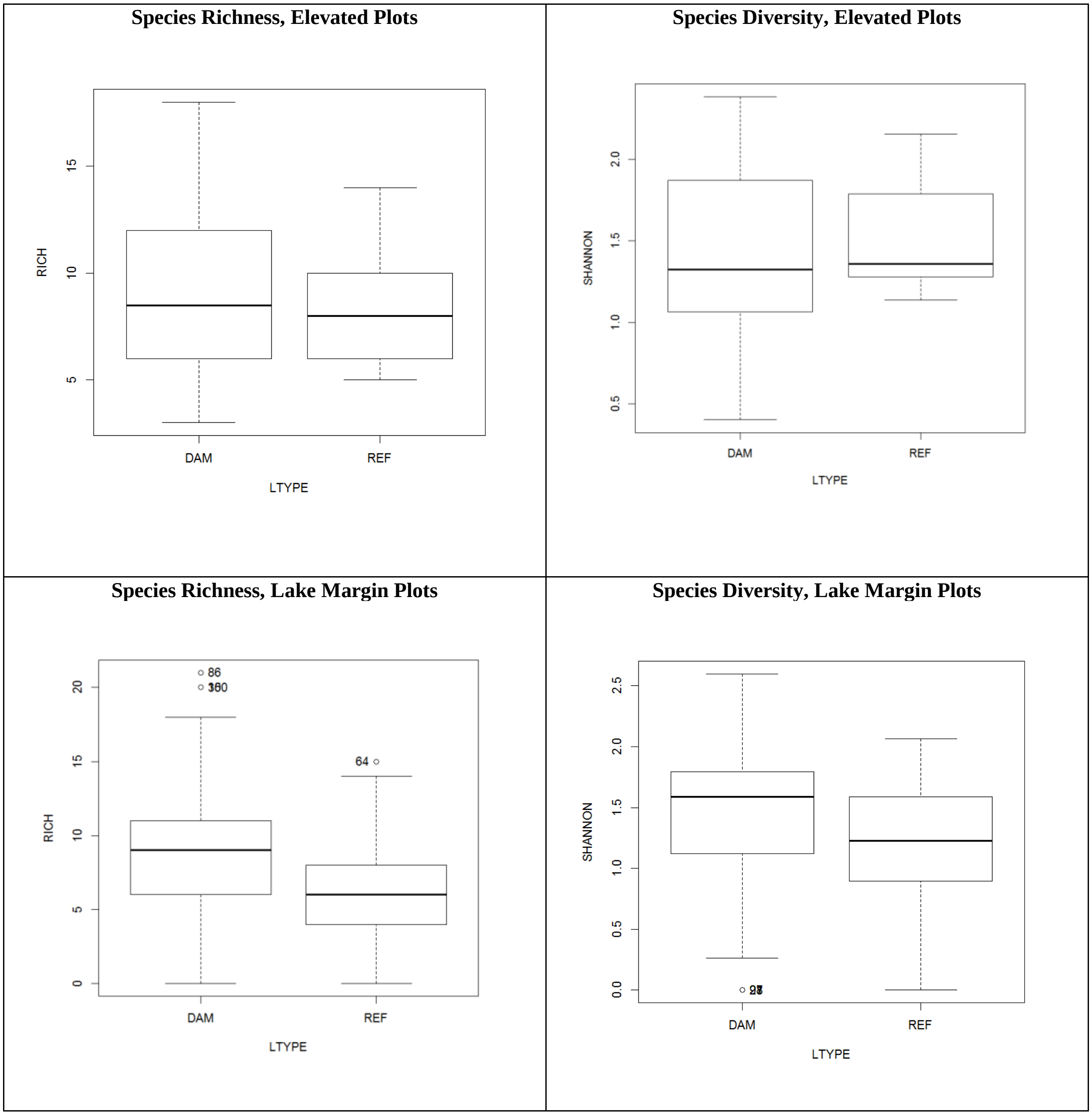

Figure 4. Boxplots comparing species richness ("RICH") and diversity ("SHANNON") data from post-dam revegetation study in RMNP, CO. Top boxplots show data from elevated plots, separated by lake type ("LTYPE" of "DAM" (formerly dammed) or "REF" (reference) in figure), bottom plots show data from lake margin plots. Points reflect outliers, occurring outside the 95th percentile. The upper and lower boundary of the box represents the 75^{th} and 25^{th} quartile.

4.2.2 *Model results*

In models comparing elevated plots at formerly dammed and reference lakes, historic damming (as identified by "lake type") did not have a significant effect on species richness or diversity. Likewise, in models comparing lake margin plots at both lake types, historic damming did not have a significant effect on diversity. However, historic damming was found to have a significant effect on species richness in lake margin plots, with previously inundated lake margin plots at formerly dammed lakes presenting an average species richness value of +3.361 greater than that measured in lake margin plots at reference lakes. A likelihood ratio test between models with and without the fixed effect of lake type (formerly dammed or reference) showed that this difference in means was statistically significant (χ^2=8.919, p=0.003). Table 5 summarizes model results.

Table 5. Observed effect of lake type (formerly dammed vs. reference) on species richness and diversity data, by plot type (elevated/lake margin). Asterisks indicate significant differences in mean between formerly dammed and reference lake types at alpha=0.05. Significance codes: '***'= 0.001; '**'=0.01, '*'=0.05, '-'=not significant.

Plot type | Dependent Variable	**Effect (Lake type = Dammed)**	**χ^2**	**p-val**	**Sig.**
Elevated | Richness	+0.5481	0.0721	0.7883	-
Elevated | Diversity	-0.2489	2.506	0.1134	-
Lake margin | Richness	+3.3608	8.9193	0.0028	**
Lake margin | Diversity	+0.3908	3.4123	0.0647	-

4.3 VEGETATION COMMUNITY CLASSIFICATION, ORDINATION, AND CORRELATION WITH SITE-SPECIFIC VARIABLES

NMS ordination of all plots combined resulted in a three-dimensional solution with a final stress of 20.424 and an instability of 0.0008. The total percent of variance in vegetation community composition explained by this ordination was 88.6%. This was the sum of the percent variation explained by each of the three axes (16.3%, 25.9%, and 46.4%). Slope was the most explanatory environmental variable with a cumulative r^2 value of 0.18, and was most strongly correlated with axes two and three (r^2= 0.042 and 0.12, respectively). Axis one was most strongly correlated with both plot elevation and elevation above waterline (r^2=0.068 and 0.058, respectively). A scree plot comparing model stress at different dimensionalities is shown in Figure 5, and two-dimensional joint plots with vectors for the environmental variables correlated with axes from the final NMS ordination are shown in Figure 6 and Figure 7. Bar graph and histogram visual frequency comparisons of categorical environmental variables by vegetation community groups are shown in Figure 8.

It should be noted that, although this final model did stabilize early in the testing process (between iterations 20 and 30 of 200), the final stress remaining is in a high enough range that test performance can only be considered “fair,” and further interpretation of results should take this caution into account.

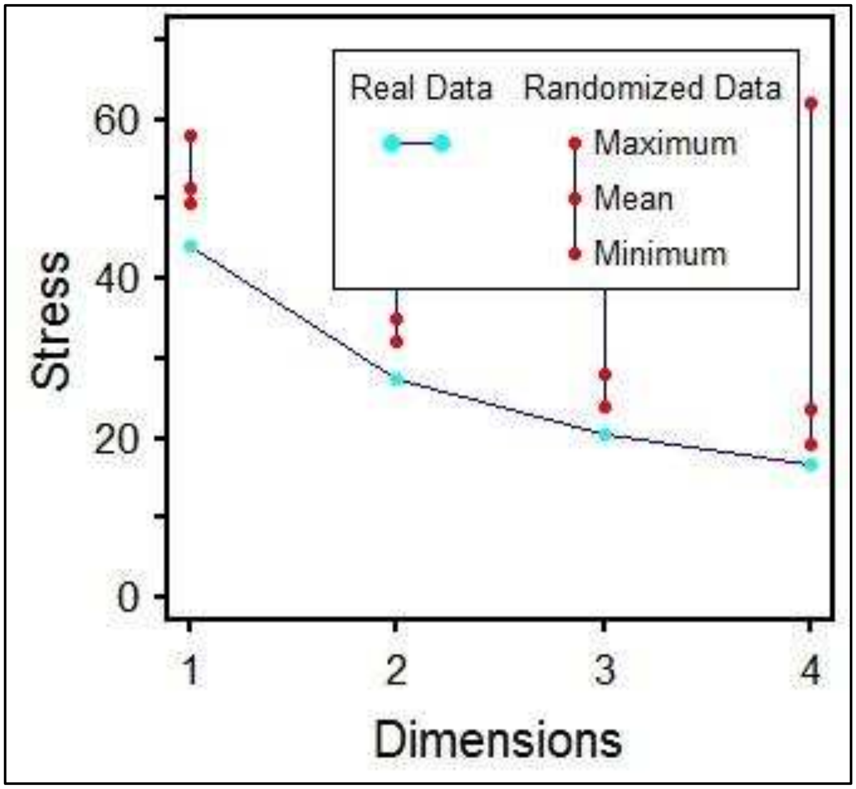

Figure 5**.** Scree plot of NMS ordination correlating variation in vegetation community composition with measured environmental variables in post-dam removal revegetation study in RMNP, CO. Scree plot was used to select the final number of axes included in the model (3). The relationship of reduction in stress to the number of dimensions included in the model is shown for both real and randomized data.

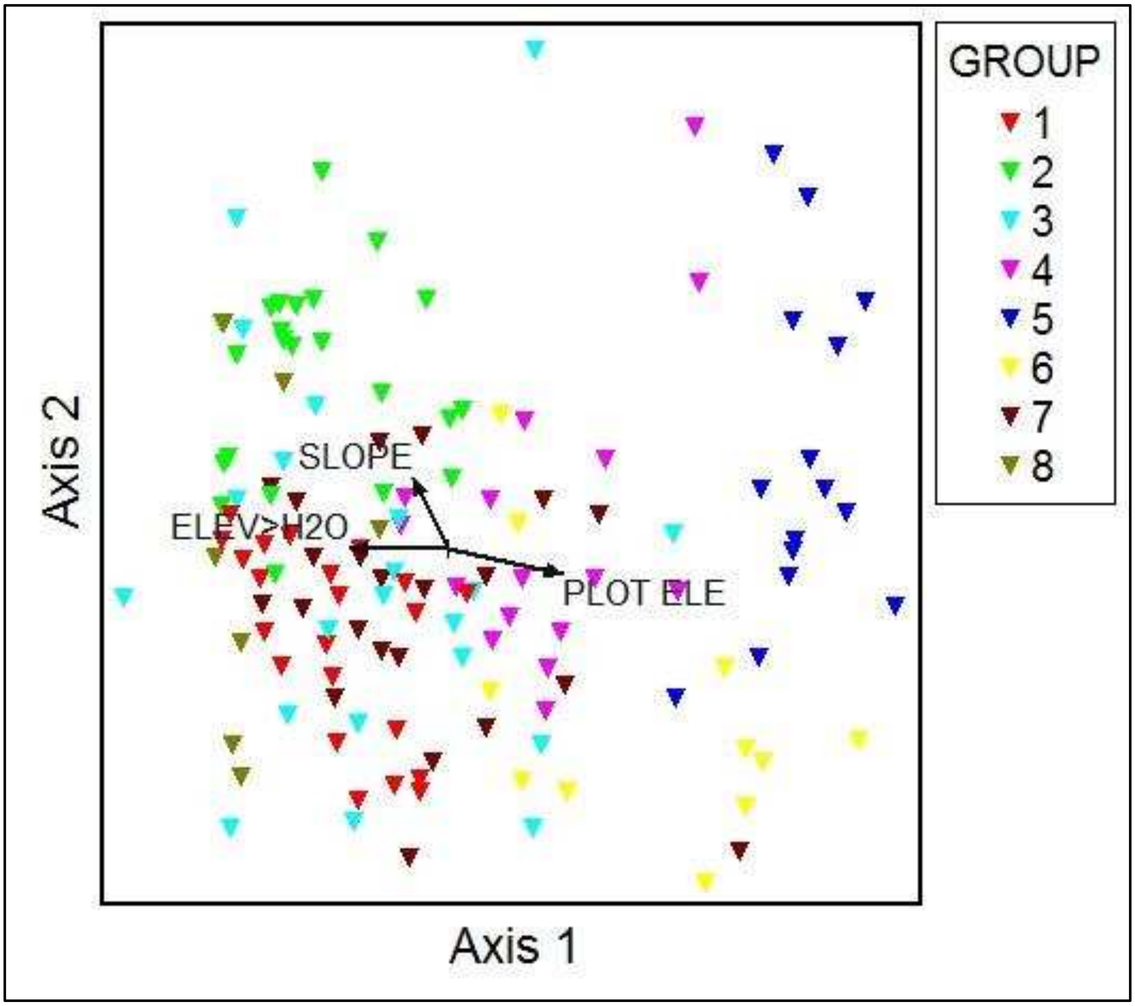

Figure 6**.** 2-D diagram of NMS ordination correlating variation in vegetation community composition with measured environmental variables in post-dam removal revegetation study in RMNP, CO. Diagram includes all plots (Axes 1 and 2), with environmental variables slope, elevation, and elevation above current waterline (ELEV>H2O) shown as vectors (r^2 cutoff = 0.04). Plots are color coded by vegetation community type as determined by hierarchical cluster analysis ("Group" 1-8 in key; further detail for each community type is included in Table 6). Arrows point toward positive correlations.

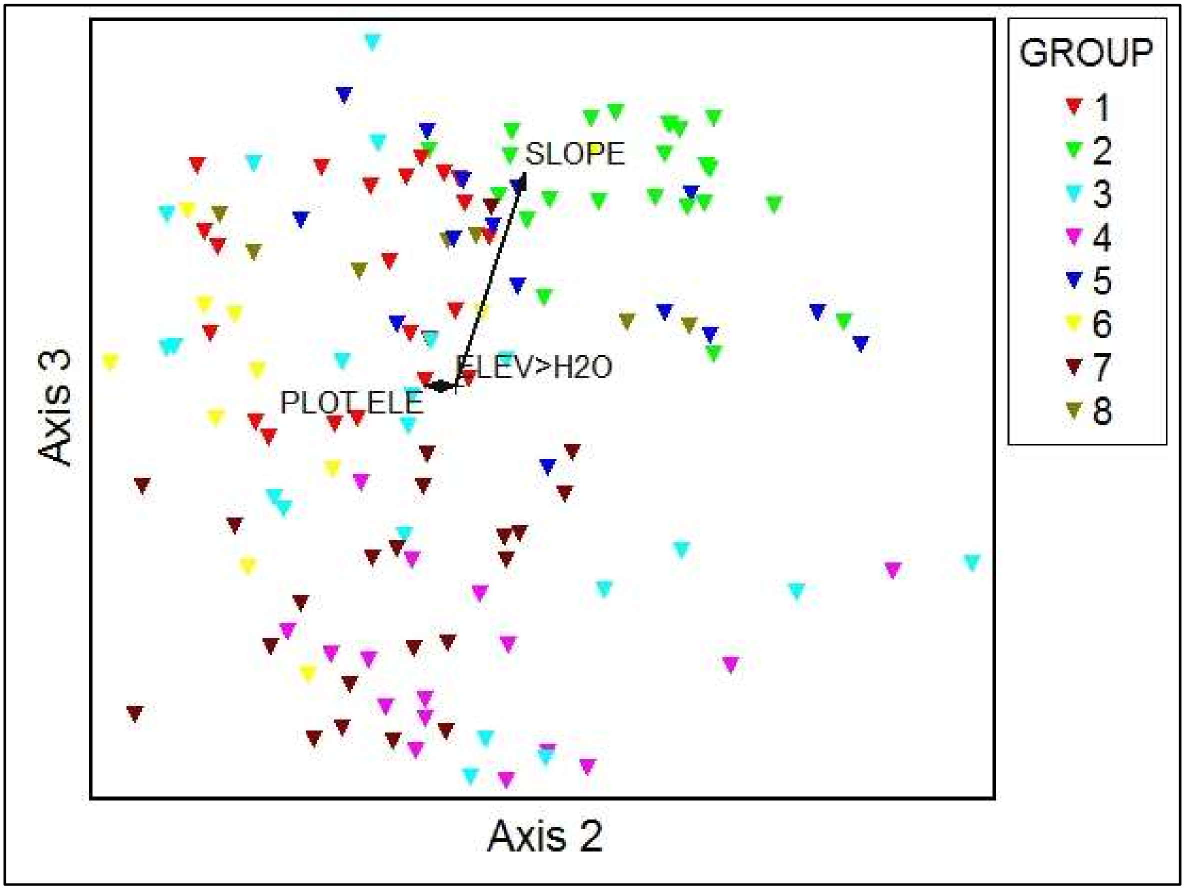

Figure 7. 2-D diagram of NMS ordination correlating variation in vegetation community composition with measured environmental variables in post-dam removal revegetation study in RMNP, CO. Diagram includes all plots (Axes 2 and 3), with environmental variables slope, elevation, and elevation above current waterline (ELEV>H2O) shown as vectors (r^2 cutoff = 0.04). Plots are color coded by vegetation community type as determined by hierarchical cluster analysis ("Group" 1-8 in key; further detail for each community type is included in Table 6). Arrows point toward positive correlations.

Bar graph of aspect frequency by vegetation community group	Histograms of frequency of soil texture classes by vegetation community group

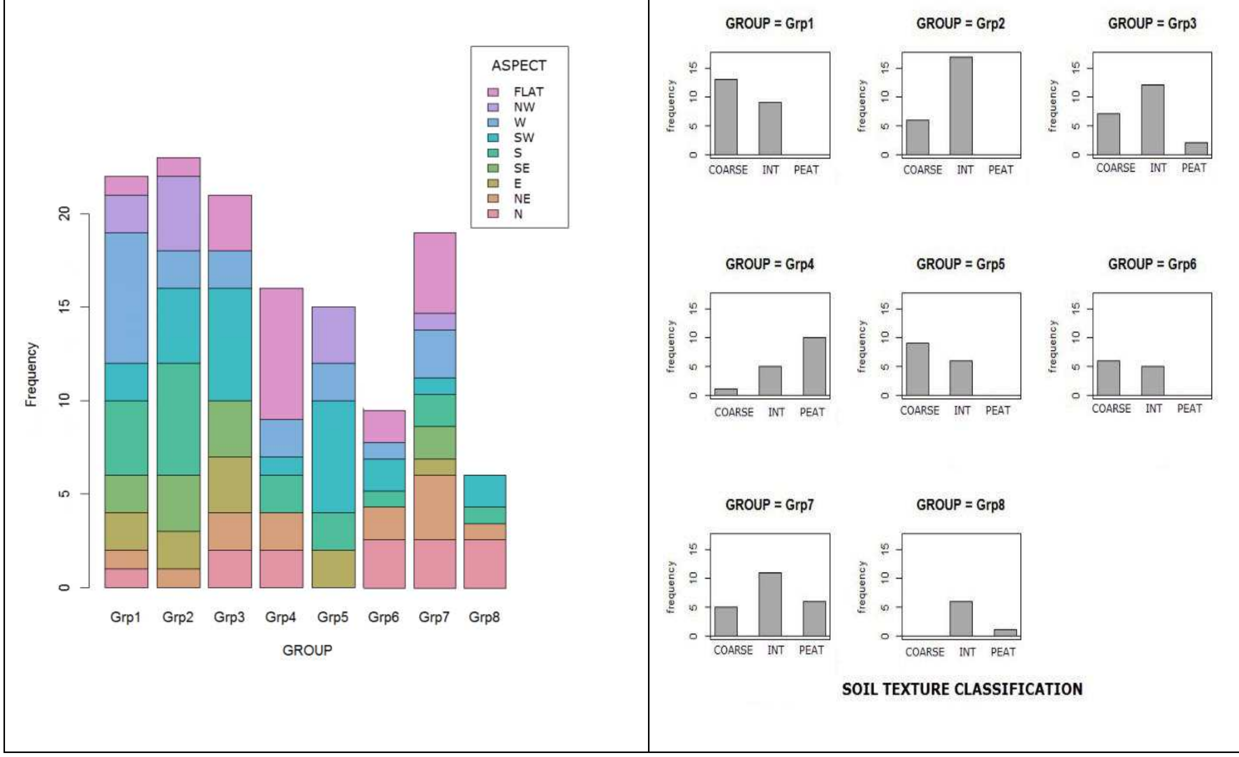

Figure 8. Bar graph and histograms showing the frequency of the categorical variables aspect and soil texture observed within each vegetation community group ("Grp" in key), in post-dam removal revegetation study in RMNP, CO. Aspect is binned into nine categories (flat, NW, W, SW, S, SE, E, NE, and N); soil texture classifications include coarse, intermediate, and peaty. Further details for each of the eight plant communities are included in Table 6.

All eight communities identified occurred at both formerly dammed and reference lake sites. Seven of the eight community types occurred in both elevated and lake margin plot types; observations of only the *Carex aquatilis – Pedicularis groenlandica* community were limited to lake margin plots. Further detail for each community, including name/number, average within-group MRPP distance, a count of elevated and lake margin/previously submerged plots within which each group was observed, and mean (±) standard error of measured environmental variables is shown in Table 6.

Table 6. ID numbers and names of eight vegetation community types identified in hierarchical cluster analysis, MRPP average within-group distance, and mean (±) standard error of measures environmental variables for each community. Community types were named according to the two or three species most prominent in each community, based on their high indicator values, their high frequency or abundance within that specific community type, or both.

Plant Community Name and Group ID Number	**MRPP within-group distance**	**n = (Elevated Plots)**	**n = (Lake Margin Plots)**	**Elevation (m)**	**Elevation > Waterline (m)**	**Slope (%)**
(1) *Picea engelmannii - Pinus contorta*	0.579	2	20	3167.45 ± 18.64	2.515 ± 0.513	22.409 ± 2.738
(2) *Abies lasiocarpa - Polemonium pulcherrimum*	0.622	9	14	3176.567 ± 20.924	4.775 ± 0.563	32.174 ± 3.855
(3) *Calamagrostis canadensis - Anaphalis margaritacea*	0.907	2	19	3170.4580± 21.576	3.145 ± 0.487	22.286 ± 4.458
(4) *Carex aquatilis - Pedicularis groenlandica*	0.669	0	16	3189.63 ± 30.215	2.92 ± 0.872	5.563 ± 1.785
(5) *Arenaria fendleri - Festuca brachyphylla*	0.888	3	12	3262.107 ± 27.217	1.62 ± 0.561	23.667 ± 5.537
(6) *Carex arapahoensis - Juncus drummondii*	0.81	1	10	3291.313 ± 19.22	2.536 ± 0.63	21.727 ± 6.39
(7) *Salix planifolia - Pyrola chlorantha*	0.679	4	13	3264.03 ± 21.146	3.722 ± 0.807	15.227 ± 3.673
(8) *Vaccinium scoparium - Erigiron peregrinus*	0.546	1	3	3252.899 ± 26.102	3.978 ± 0.96	30.143 ± 5.434

4.4 COMPARISONS OF NATIVE AND NON-NATIVE SPECIES PRESENCE

Species were classified as “native,” “introduced,” or “both” (both native and introduced populations exist in the area), following classification utilized by the USDA Plants Database (USDA NRCS 2015). Only one species observed, *Rumex acetosella*, was listed in the USDA database as strictly “introduced” in this area of the Rocky Mountains, occurring in a total of five plots (comprising 3% of all plots, 3% of all lake margin/previously submerged plots, and 4% of all elevated/never submerged plots). *Rumex acetosella* occurred in three plots at three different lake sites including formerly dammed and reference lakes (Mills Lake, Loch Vale, and Sandbeach Lake), and ranged from 10-12% canopy cover (11-22% of the total canopy cover observed in each plot where the species occurred). The plot at formerly dammed Sandbeach Lake in which *Rumex acetosella* was observed was lake margin (previously submerged); both other plots occurred at reference lakes and so, by definition, were not ever subject to historic damming disturbance. One of these plots was an elevated plot at Mills Lake; another was one of the plots sampled at Loch Vale that were lacking elevation data.

Four other species observed were classified by the USDA Plants Database as “both” (both native and introduced populations exist in the area), including *Cerastium arvense* (1 plot), *Streptopus amplexifolius* (1 plot), *Taraxicum officinale* (5 plots), and *Rubus idaeus* (9 plots). When these species were also included in summary evaluation, the number of plots where possibly non-native species were observed rose to 17, including seven at Pear Lake, two at Sandbeach Lake, and two at Bluebird Lake (formerly dammed lake sites, with all observations occurring in lake margin/previously submerged plots); and three at Lake Haiyaha, two at Mills Lake, and one each at Loch Vale and Thunder Lake (reference lake sites). No non-native species were observed at either Eagle or Lawn Lakes (a reference and a formerly dammed lake site, respectively).

The issue of native/non-native classification is further obscured by differing classifications made by the Park itself. In RMNP's Invasive Exotic Plant Management Plan and Environmental Assessment (Department of the Interior 2003), 102 plant species known to occur in the Park are classified as exotic. However, while this list does include *Taraxicum officionale*, it does not list *Rumex acetosella*, nor the other three species with ambiguous USDA Plants Database classifications listed above. Given the inconsistent classifications between agencies, judging whether observations of these few species in question represent truly native or introduced populations would be subjective at best, and so any interpretation of testing focusing on the presence/absence of these species would be speculative and therefore inconclusive. Analysis beyond summary statistics was not performed.

5. DISCUSSION

5.1 EFFECTS OF HISTORIC DAMMING ON SPECIES RICHNESS AND DIVERSITY

Studies of post-disturbance revegetation conducted at alpine sites where glacial retreat has created similar conditions to those resulting from dam removal (prolonged disturbance that has potentially resulted in loss of a viable seed bank, followed by the re-exposure of unconsolidated, water-saturated sediments available for pioneering, recolonization, and succession) shed some light on the unique dynamics of revegetation in high-elevation environments. These vegetation colonization studies have documented that factors such as the shortened growing season, lower average summer and winter temperatures, winds, ice stress, potentially more limited methods of seed dispersal, and other environmental variables limiting germination, recruitment, and survival of pioneering species represent limiting factors unique to the high mountain environment (Robbins and Matthews 2009, Hagen et al. 2014). However, even though vegetation community development would be expected to follow a slower trajectory, especially in the absence of the types of active reseeding and vegetation management actions frequently used at lower elevation restoration sites, highly disturbed alpine sites do show high restoration potential via spontaneous succession processes given sufficient time, eventually exhibiting higher levels of vegetative cover and species richness than comparable study sites where seeding was performed to speed revegetation (Hagen et al. 2014).

One possible explanation of the higher species richness found in the lake margin/previously-submerged areas at historically dammed lakes compared to the richness of similar lake margin plots at reference lakes in this study may also lie in glacial foreland studies that have documented a progression from low to high species richness and diversity over a chronosequence. Because rates of glacial retreat are known and documented and therefore study areas can include a range of ages (from youngest/least developed at the glacier snout to oldest/most developed at the more distant end of the foreland), studies of revegetated glacial forelands provide a design that facilitates an examination of the relationship of time since disturbance to vegetation community characteristics, cover, and richness and diversity data

In these studies, the primary succession trajectory of colonizing vegetation has been characterized as rapid initial community development during the first 50 years following soil exposure, followed by a plateau and then drop in overall species richness (Burga et al. 2010). This post-peak stabilization at a lower overall species richness than that exhibited at the point of highest richness in the recolonization period has been linked to stochastic events, species-specific life history traits of initial colonizers (e.g., limited aging and growth potential), and evidence of eventual competitive displacement (Erschbamer et al. 2008, Burga et al. 2010, Prach and Rachlewicz 2012). In all studies, the relationship between species richness and the post-disturbance successional age of the area has been shown to be significant.

The revegetation at RMNP's formerly dammed lakes has been taking place for only 25 years. Currently elevated species richness in disturbed areas at these lakes may represent a mid-point on this successional progression; if so, species richness at formerly dammed sites might be expected to peak, and later stabilize at a level similar to that of reference lakes in another 25 years.

5.2 ENVIRONMENTAL DRIVERS OF VEGETATION COMMUNITY COMPOSITION

Literature on alpine and subalpine vegetation makes clear the importance of slope on a microclimate scale, in terms of its influence on variations in shading, solar angle and timing, and interaction with wind, gravity, and soil water retention (Körner 2003). Thus, it is unsurprising that in the high mountain context of this study, slope was found to have the strongest correlation with vegetation community classification. The influence of slope can also be linked to its interaction with exposure, which can result in contrasting thermal conditions in both air and root zones at sites with similar slopes but different exposures (e.g., north- vs. south-facing). While elevation is also known to be a significant determining factor in the overall ranges of plant species, because all plots included in this study were confined to a narrow band of elevation (within a total range of only 323 m), the weaker explanatory nature of elevation found in this study would also be expected.

5.3 UNIQUE COMMUNITY ASSEMBLAGES

Although it was necessary to remove infrequently-observed species in order to smooth out interfering “noise” in the data for cluster analysis, this type of data simplification can also obscure unusual but notable effects; this study included several such observations. In two lake margin/previously-submerged plots at Pear Lake, a formerly dammed site at an elevation of 3,227 m, *Salicaceae* species whose documented upper or lower elevation range limits are well below or above this elevation were observed, growing in stands that also included a mix of montane *Salicaceae* species. These included lower-elevation residents *Populus angustifolia* and *Salix lucida ssp. lasiandra*, whose known upper elevation range limits at this latitude are appx.

2,400 and 3,100 m, respectively, and *Salix nivalis*, generally an alpine species normally found growing at elevations above 3,500 m (Flora of North America Editorial Committee, eds. 2010).

Relatedly, a historic presence of *Populus angustifolia* seedlings in disturbed areas surrounding Lawn Lake (elevation 3,350 m), with water stress-related die-off in subsequent low-precipitation years, had been noted by RMNP personnel engaged in informal monitoring of revegetation in the initial years following that dam's failure (Connor, personal communication). If these historic observations are indicative of a pattern, they would point toward likely eventual die-off of these individuals at Pear Lake as well. However, the *Populus angustifolia* observed at Pear Lake were well beyond the drought-vulnerable seedling stage (appx. 2 to 3 m tall), and showed no signs of stress or dieback. It is possible that their early establishment and persistence through the early seral stages of succession at this lake could contribute to a unique community assemblage that will persist into the future.

The wind dispersal of *Salicaceae* seeds could explain their transport into areas distant from existing populations, while plant species with more limited seed mobility would not achieve the same range of colonization (Michel et. al 2011). The implications of species' differing abilities for seed dispersal as they relate to future climate change, temperature-driven shifts in the elevation ranges of RMNP's native species, and predictions of future community assemblages would be an interesting focus for a related study of these populations.

5.4 INVASIVE SPECIES AND ANTHROPOGENIC INFLUENCE

Aside from geographically-based environmental differences, another key difference between this dam removal study and others such as the survey of dam removals in Wisconsin (Orr and Stanley 2006) lies in the land use and management of the site following dam removal. More than half of the recovered areas included in a survey of Midwestern dam removals were converted to intensively-managed uses such as parks, agricultural land, or commercial areas, where an early and extensive establishment of aggressive invasive species was frequently observed (Orr and Stanley 2006). In notable contrast, the dam removal sites in RMNP were not actively managed and yet, do not appear to have been affected by the establishment of non-native invasives to the degree that dam removal studies made in lower elevation and higher-use areas would predict. This can likely be attributed to two factors: the harsher environmental limitations posed by high mountain systems, which could be expected to curtail invasion by any generalist ruderal not adapted specifically to the extremes of this environment (Körner 2003, McDougall et. Al 2005); and the relationship between invasive plant richness and high anthropogenic disturbance (Gassó et al. 2009).

In fact, in RMNP's own Park-wide environmental assessment for the development of its exotic plant management plan, areas identified as having the highest levels of exotic infestations are highly correlated with the areas of the Park that experience high levels of visitor use and impact, with *"people, machinery, vehicles, and livestock"* expressly listed as contributors to the establishment and spread of non-native vegetation within the Park. At more remote sites such as those included in this study[5], it is reasonable to conclude that the comparatively low incidence of invasive species observed is related to the relatively limited opportunity for human-caused disturbance and dispersal of invasive propagules, as compared to that which occurs with higher frequency in more developed, well-visited areas of the Park (such as that from roadside

[5] It should be mentioned that the Glacier Basin frontcountry campground area of RMNP was included in the Park's EA as an area of concern for the control of invasive exotics. Adjacent Glacier Gorge, where three of this study's reference lake sites are located (Lake Mills, Loch Vale, and Lake Haiyaha), is home to one of RMNP's most-used short trail systems, which visits all three of these reference lakes. Although the Park does not maintain specific trail use statistics, in 2015 RMNP's visitor count exceeded 4 million.

disturbance, establishment of social trails, and the impacts of stock animal travel, feed, and feces) (Department of the Interior National Park Service, Rocky Mountain National Park 2003).

5.5 SHORTCOMINGS OF THIS STUDY AND SUGGESTIONS FOR FUTURE STUDIES

A review of the means of measured environmental variables for each vegetation group identified in cluster analysis (Table 6) can potentially confuse the intuitive association between elevation above waterline, water availability, and the hydrophytic plant classification (i.e., obligate wetland, facultative wetland, facultative, and facultative upland plant classifications) of each vegetation community's prominent species. This is likely due to variation in water availability caused by site-specific factors such as hillside groundwater seep or local surface water accumulation, which would not necessarily correlate with any elevation measurement. Measurement of soil moisture at each plot might have provided more relevant clarifying information in NMS.

Measures of cover were not divided into overstory and understory categories in this study, which might have provided an additional explanatory variable in NMS and for overall evaluation of canopy cover differences. Additionally, this study did not measure the height structure of canopy observed, which could better inform the overall differences still visually apparent in plots where conifer-dominated communities have reestablished in previously submerged areas. Where slow-growing species such as *Picea engelmannii* have recolonized, the canopy structure is very different from older undisturbed stands that were classified into the same vegetation community group (i.e., recolonized stands showed a higher percent cover in their understory, which might be expected to change as overstory canopy and shading increases with increased age and height of trees). However with the specific data measured for this study, it was not possible to quantify these differences.

One-time relevé surveying of vegetation is informative as a “snapshot” of current outcomes of passive restoration, but its utility in speaking to past and future seral progression of these sites is limited. Repeated monitoring visits to the same sites year after year would lend more insight into the processes that continue to unfold at these formerly dammed lakes, but would likely be a prohibitively expensive undertaking, and permanently marking survey plots in the backcountry would run counter to current NPS management philosophy. “Citizen science” approaches to similar monitoring challenges are being utilized elsewhere to gather information on rangeland vegetation and riparian conditions (most notably, a USGS-partnered student initiative on a stretch of the South Fork Boise River east of Boise, ID, involving installation of fixed photo-point brackets where visitors are encouraged to place their cameras, take a photo, and upload it with a specific hashtag so that it can be “harvested” to a collective database for use in a time-lapse sequence). Because RMNP is so well-visited, a similar approach inviting visitors to voluntarily contribute to such a long-term fixed-photo documentation project could prove informative (in addition to furthering the Park’s educational and interactive missions). Though such a project would likely not provide detailed species composition data, more general trends in vegetation change could become apparent in these collections of photographs, especially if continued over a time scale of decades.

6. CONCLUSION

This study found that although historic damming did not have observable effects on the vegetation in elevated areas surrounding RMNP's high mountain lakes 25 years after dam removal, the four study lakes with a history of damming disturbance have significantly higher species richness in their previously-submerged areas, as compared to lake margin areas at reference lakes with no history of damming. Similar environmental conditions and vegetation communities are found at both formerly dammed and reference lakes, with slope and elevation being the measured environmental variables showing the strongest correlation to vegetation community types.

The results of this study highlighted both similarities to, and differences from, existing literature on post-disturbance vegetation community development as it relates to damming and dam removal. These differences hinge on this study's location in a differing ecosystem than those previously researched. In contrast to studies of dam removals and reservoir drawdowns that have observed a rapid and often monotypically-inclined nonnative revegetation outcome in the years immediately following a low elevation dam removal, or in water level fluctuation zones of low elevation reservoirs during prolonged (multi-year) drawdowns (Orr and Stanley 2006, Auble et al. 2007, Peng et al. 2014), the alpine/subalpine locations of this study's sites present different influences and challenges to vegetation community development, resulting in different outcomes.

The passive revegetation approach employed by RMNP following dam removals can be seen as successful in terms of species diversity and overall vegetation cover, although a consideration should be given to the time scale required for full restoration in high mountain ecosystems. It is likely that these sites will continue to undergo changes as succession continues.

This study’s conclusions support the use of a passive revegetation approach for restoration in disturbed high mountain ecosystems. Continued monitoring of these sites would further expand understanding of the long-term trajectory of unassisted primary succession following severe disturbance in high mountain ecosystems.

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APPENDIX A: List of vascular plant species observed in surveyed plots. "*" denotes species that were classified as "infrequently observed" (occurrence in < 3 plots), and were omitted from cluster analysis.

Apiaceae
Conioselinum scopulorum
*Heracleum maximum**
*Ligusticum porteri**
*Osmorhiza depauperata**

Asteraceae
Achillea millefolium
*Agoseris glauca**
Anaphalis margaritacea
Antennaria rosea
Arnica cordifolia
*Arnica latifolia**
Arnica mollis
*Artemesia scopulorum**
Cirsium scopulorum
*Erigeron coulteri**
Erigeron peregrinus
Erigeron pinnatisectus
Hieracium gracile
*Packera cana**
*Senecio crassulus**
*Senecio fremontii v. blitoides**
Senecio triangularis
Solidago simplex
Taraxacum officinale
*Tetraneuris grandiflora**
*Tonestus pygmaeus**

Betulaceae
Betula glandulosa

Boraginaceae
Mertensia ciliata

Brassicaceae
*Cardamine cordifolia**
Draba fladnizensis

Caprifoliaceae
*Linnaea borealis**
Lonicera involucrata
*Sambucus racemosa**

Caryophyllaceae
Arenaria fendleri
*Cerastium arvense**
*Minuartia rubella**
*Paronychia pulvinata**
*Silene acaulis**
*Stellaria calycantha**

Crassulaceae
*Rhodiola integrifolia**
Rhodiola rhodantha
Sedum lanceolatum

Cupressaceae
Juniperus communis

Cyperaceae
Carex aquatilis
Carex arapahoensis
*Carex brunnescens**
Carex canescens
*Carex disperma**
Carex elynoides
*Carex filifolia**
*Carex geyeri**
*Carex illota**
*Carex micropoda**
Carex nigricans
*Carex pellita**
*Carex praeceptorum**
*Carex rossii**
Carex scopulorum
Eleocharis quinqueflora

Ericaceae
Gaultheria humifusa
Kalmia microphylla
Vaccinium cespitosum
Vaccinium myrtillus
Vaccinium scoparium

Gentianaceae
*Gentiana affinis**
Gentiana algida
*Gentiana parryi**
Gentianella amarella s. acuta
Swertia perennis

Grossulariaceae
*Ribes coloradense**
*Ribes inerme**
*Ribes lacustre**

Juncaceae
Juncus drummondii
*Juncus hallii**
Juncus mertensianus
*Juncus parryi**
*Juncus triglumis**
Luzula parviflora
Luzula subcapitata

Liliaceae
*Streptopus amplexifolius**

Onagraceae
Chamerion angustifolium
Epilobium saximontanum

Orchidaceae
*Listera cordata**
Platanthera dilatata

Pinaceae
Abies lasiocarpa
Picea engelmannii
Pinus contorta
Pinus flexilis

Poaceae
Agrostis humilis
*Agrostis idahoensis**
*Agrostis scabra**
*Bromus carinatus**
Calamagrostis canadensis
*Danthonia intermedia**
Deschampsia cespatosa
Festuca brachyphylla
*Helictotrichon mortonianum**
Phleum alpinum
Poa alpina
*Poa fendleriana**
Poa interior
Poa leptocoma
*Poa palustris**
*Poa reflexa**
Poa secunda
Trisetum spicatum

Polemoniaceae
Polemonium pulcherrimum
*Polemonium viscosum**

Polygonaceae
Oxyria digyna
Polygonum bistortoides
Rumex acetosella

Pyrolaceae
*Pyrola asarifolia**
Pyrola chlorantha
*Pyrola minor**
*Pyrola secunda**

Ranunculaceae
Anemone narcissiflora
*Aquilegia coerulea**
Caltha leptosepala
*Delphinium ramosum**
*Trollius laxus**

Rosaceae
Pentaphylloides floribunda
Potentilla gracilis
Potentilla ovina
Rubus idaeus
Sibbaldia procumbens

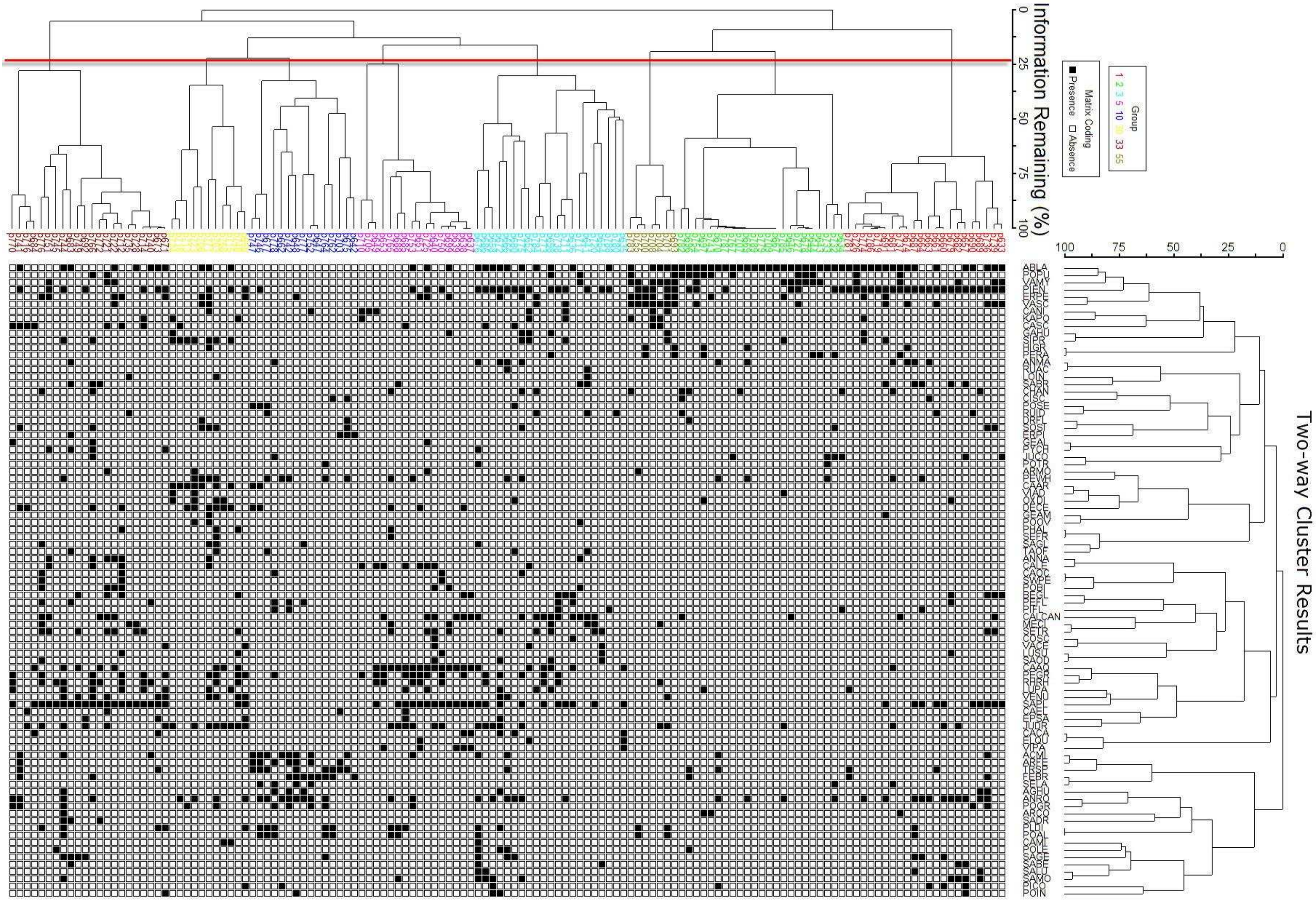
Salicaceae
*Populus angustifolia**
Populus tremuloides
Salix bebbiana
*Salix boothii**
Salix brachycarpa
Salix drummondiana
Salix geyeriana
Salix glauca
Salix lucida ssp. lasiandra
Salix monticola
*Salix nivalis**
Salix planifolia
*Salix wolfii**

Saxifragaceae
*Saxifraga nivalis**
Saxifraga odontoloma

Scrophulariaceae
Castilleja occidentalis
*Pedicularis bracteosa**
Pedicularis groenlandica
Pedicularis racemosa
Penstemon whippleanus
Veronica nutans

Violaceae
Viola adunca
Viola palustris

APPENDIX B: Two-way cluster matrix output, showing species presence/absence for each plot and the dendrogram grouping of plots into eight final community types.



APPENDIX C: Representative photos of vegetation communities identified in cluster analysis

Picea Engelmannii - Pinus contorta

Calamagrostis canadensis - Anaphalis margaritacea

Arenaria fendleri - Festuca brachyphylla

Abies lasiocarpa - Polemonium pulcherrimum


Carex aquatilis - Pedicularis groenlandica


Carex arapahoensis - Juncus drummondii

Salix planifolia - Pyrola chlorantha

Vaccinium scoparium - Erigeron peregrinus