

Environmental Variation and Vegetative Composition in Beaver Engineered Ecosystems

Eva McDonough, 2024 Undergraduate Education Program

Mentor: Dr. Ian Breckheimer

Rocky Mountain Biological Laboratory

August 9th, 2024

ABSTRACT

The Colorado Rocky Mountains are uniquely heterogeneous, with beaver-engineered wetlands being sites with especially high relative biodiversity. Despite the large body of research available on the impacts of beaver activity on wetlands, the specific mechanisms of beaver activity that create high plant biodiversity in this unique disturbance regime are poorly understood. As beaver reintroduction, BDAs, and the implementation of wetland restoration gain popularity, it is important to understand the mechanisms that make beavers such powerful ecosystem engineers, and why those engineering efforts are so effective at promoting diversity. This research explored the role of temporal environmental variability, as measured using uncrewed aircraft system (drone) data, in maintaining the unique vegetation communities present in beaver ponds. While there were no significant differences in plant alpha diversity found between stable and highly variable ponds, multivariate ordination techniques (non-metric multidimensional scaling and PERMANOVA) showed significant differences in the community composition based on variability. The findings underscore the complexity of beaver pond ecosystems and suggest that a mosaic of factors contribute to the heterogeneity of beaver pond vegetation.

INTRODUCTION

Wetlands, especially beaver-engineered ones, harbor a disproportionately high biodiversity despite the relatively small area they occupy (Law, 2019). The introduction of beavers and, more recently, the implementation of Beaver Dam Analogs (BDAs) are increasingly popular conservation strategies that combat declines in wetland health and protect the unique species composition found in beaver ponds (Hill, 2023). Wetland ecosystems, which are extremely heterogeneous, have shown more phenological stability than other ecosystems at large scales (Dronova, 2022). Along with having high phenological stability, wetlands engineered by beavers are more adaptable to flooding and drought, a sign of resiliency in a rapidly changing climate (Law, 2019). Beaver ponds hold more water per unit area than other wetlands, with this phenomenon being even more pronounced in drought conditions (Fairfax, 2017). As the climate

continues to change, water resources are projected to become even more scarce in the western United States, an issue that ecosystem engineering may help with.

Beyond the positive ecosystem services beavers provide hydrologically, there is also increased biodiversity seen in these ecosystems (Brazier, 2021). The unique physical structure of beaver ponds, which is typically shallower than other water bodies, contributes to the high level of biodiversity present in terrestrial plants, aquatic plants and water beetles (Scarmando, 2019). In addition to structural alterations, the foraging habits of beavers promote increased biodiversity through novel disturbances to the landscape (Rakowska, 2023). A limited number of studies demonstrate the ability of beavers to increase biodiversity through increased environmental variation (Willby 2018, Law 2019, Dronova 2022). Existing research indicates that the number of unique plant species in active beaver ponds is 50% greater than in wetlands uninfluenced by beavers (Willby, 2018). Willby (2018) attributes part of this increase in species to an increase in patch size and turnover in beaver-maintained wetlands, which is due to small-scale disturbance (Willby, 2018). The disturbance regime created by beavers favors species adapted to highly variable environments, meaning that a variety of species that otherwise might not be successful could take root (Law, 2019).

Beaver created disturbance is linked to biodiversity through the creation of microhabitats at different successional stages (Burgher, 2023) Microhabitats can support a variety of species with different environmental requirements. Beaver behavior fosters the creation of microhabitats and therefore the diverse habitat structures which support a range of organisms (Rakowska, 2023). Another mechanism through which disturbance promotes biodiversity is through preventing restrictions in species diversity due to competitive exclusion (Bonner, 2008). A few species may be able to dominate stable environments as they are well-adapted to the specific conditions which consistently present. Disturbances provide the opportunity for other species, which may not be as competitive to establish themselves as new niches are created (Dornelas, 2010).

The composition of the vegetative community is a key component that determines the efficacy of wetland ecosystem services (Brazier, 2021). An assessment of the specific mechanisms that promote heterogeneity in the vegetative community may provide insights into areas of improvement for wetland restoration, such as further conservation work focused on the recruitment of key vegetative species (Houlahan, 2006). Ecological variability and dynamics within beaver pond complexes are poorly understood, whereas the comparison between beaver and non-beaver sites has been extensively studied. More research is needed to uncover the specific mechanisms contributing to the high biodiversity of beaver ponds and to identify which pond characteristics promote increased biodiversity.

To address the gaps in understanding surrounding beaver pond vegetation dynamics, this study seeks to answer the question, how does temporal environmental variability of beaver ponds influence the vegetation community? Existing research indicates that the high degree of temporal and spatial environmental variation in beaver ponds may be a key factor in explaining the high relative biodiversity. I hypothesize that if temporal variability plays a strong role in promoting plant biodiversity in beaver ponds, highly variable ponds will exhibit higher plant species richness than stable ponds. This hypothesis is based on the premise that greater environmental variability within beaver ponds creates more disturbances, which may contribute to higher levels of biodiversity.

METHODS

Remote Sensing Analyses

A multiscale approach was used to determine the effects of environmental variation of ponds on vegetative diversity and composition. A representative orthomosaic from June 15th, 2022, was used to delineate the beaver ponds present within the Gothic Townsite drone flight path (Appendix 1). Polygons representing each beaver pond were created by using the visible boundary between open water and emergent vegetation to delineate the perimeter of the shape. There were 64 different ponds defined (every pond visible from the drone imagery, greater than 4m), all located across the East River from the Gothic Townsite. The ponds were grouped into South, Middle, or North locations, with 18 ponds being in the southern group, 28 ponds being in the middle group, and 18 ponds being in the northern group (Appendix 1, Appendix 2). The ponds were then numbered for easier identification.

Study Site Selection

The weekly record of Gothic Townsite drone data from 2022 collected by the RMBL Spatial Ecology Lab was used to characterize the temporal stability of each pond in terms of surface temperature (°C) and Normalized Difference Vegetation Index (NDVI), a measure of vegetation cover that is also sensitive to the amount of open water. RGB and multispectral-thermal orthomosaics were derived from RMBL's DJI m300 RTK UAS system and DJI P1 RGB camera and Mica sense Altum multispectral sensor. Orthomosaics were generated at high spatial resolution (1-5 cm/pixel) and very high geospatial precision (3-5 cm). The drone was operated at an altitude of 100m, taking photos every ~1 seconds along flight paths spaced 20m apart across the study area, resulting in roughly 4600 images of the Gothic Townsite per flight for both the RGB and multispectral sensors. The images have a horizontal and vertical overlap of approximately 80% and were orthorectified and mosaiced in Agisoft Metashape version 1.7.

There were 22 orthomosaics evaluated from April 2022 to October 2022. A high degree of variation in pond surface area, temperature, and NDVI was seen across ponds, which made site

selection complex (Figure 1). To capture more dimensions of variation across time, the standard deviation of both temperature and NDVI was evaluated during the pond selection process. Five ponds were randomly selected in the 70th percentile or higher for standard deviation and designated as "variable," and five ponds in the 30th percentile or lower for standard deviation were designated as "stable" (Figure 1). The size and geomorphic setting were matched as much as possible between the two study groups. The randomized selection of ponds within the specific variability categories allowed for a representative sample of ponds to be selected for on-the-ground sampling (Figure 2). The selection of ponds was limited by the potential for separation between individual plots (minimum 2m) and ease of access. The spatial variation across ponds was visualized by mapping each pond and its specific temperature and NDVI values (Figure 3).

Field Sampling

Field data collection occurred from July 11th to July 30th. Each of the ponds selected had a minimum of eight 50cm by 1m plots randomly spaced along the pond edge with a minimum spacing of 2m to ensure independence of samples (Figure 4). Exceptions to the plot selection procedure included the removal or an adjustment of location for plots where 2m spacing was not possible, or the plot was inaccessible. A total of 77 plots were sampled across ten individual ponds. Each plot was defined using a 50cm by 1m quadrat, the size of which was chosen to maximize species cover evaluations while maintaining sampling efficiency. The short edge (50cm) of the quadrant aligned with the boundary between open water and emergent vegetation. The quadrat was placed to avoid covering areas of open water, containing disconnected islands of vegetation, or being directly on top of beaver dams. Within the 50cm by 1m quadrat, an evaluation of species richness was taken by first identifying the species present in the plot and then quantifying the percent cover of each species by ocular estimation.

Only emergent plants were identified, and each species was identified to the lowest feasible taxonomic level. Species guides, primarily the Colorado Wetlands Initiative Common Wetland Plants of Colorado's Southern Rocky Mountains (Culver, 2020), were used to assist in plant identification as well as further identification through consultation.

General observations of hydrology and beaver activity were taken along with the maximum height for each functional group in the plot and the maximum water depth within the plot. Beaver activity, such as evidence of foraging and beaver structures, was taken note of at each site. Each site was also characterized in terms of alignment with beaver dams. In general, the beaver dams were aligned with the downslope (East) edge of each pond and followed the topographic characteristics of the area.

Data Processing

The site characteristics derived from drone imagery, species composition data, and field site characteristics were compiled in a master spreadsheet before being analyzed. The Shannon Diversity Index was calculated for each plot using the percent cover of each species and the total composition of all species within each plot (see equation below). The Shannon Index for each plot was amended to the existing data for further analysis.

$$-\sum \left(\frac{\text{cover_pct}}{\sum \text{cover_pct}} \times \log \left(\frac{\text{cover_pct}}{\sum \text{cover_pct}} + 1 \times 10^{-10} \right) \right)$$

Statistical Analyses

A Bayesian generalized linear mixed model (R.4.4.0 rstanarm) was then used to evaluate the effect of variability category, pond area, temperature standard deviation, NDVI standard deviation, and plot alignment on the Shannon Index of each plot. Non-metric Multidimensional Scaling (NMDS) was used for the species composition and abundance data (R.4.4.0 vegan). The Bray-Curtis distance metric used for the NMDS. A Permutation-based Multivariate Analysis of Variance (PERMANOVA) test was used to evaluate the significance of variability, plot alignment, and pond area as grouping variables (R.4.4.0 vegan).

RESULTS

Gothic Townsite Pond Characteristics

A large degree of environmental variation was observed in the Gothic Townsite beaver ponds based on data derived from 2022 drone imagery (Figure 1, Figure 3). The temporal variation of ponds included an average temperature standard deviation of 8.38 degrees Celsius, whereas the mean temperature was 6.78 degrees Celsius. The standard deviation of the NDVI observed in the beaver ponds was 0.0427 compared to a mean of 0.168.

To determine the potential influences on temperature and standard deviation across time and space, potential covariates were plotted with each of the pond characteristics. The most significant factor in determining pond characteristics was their water surface area as derived from drone imagery (Figure 5). Pond area had a moderate negative correlation with mean temperature ($R^2 = 0.35$), mean NDVI ($R^2 = 0.34$) and temperature standard deviation ($R^2 = 0.34$). Pond area and temperature metrics had a negative relationship, as did pond area and mean NDVI. There was a very weak correlation between pond area and NDVI standard deviation ($R^2 = 0.06$), though a slight positive relationship still existed. Mean temperature had a very strong positive correlation ($R^2 = 0.75$) with temperature standard deviation. Mean NDVI also had a

correlation with NDVI standard deviation, though the relationship was less strong ($R^2 = 0.56$) and quadratic.

Vegetation Composition Compared to Environmental Characteristics

The mean Shannon Index for stable ponds was 2.36, and the mean Shannon Index for variable ponds was 2.40. The standard deviation between the two groups differed slightly, with stable ponds having a standard deviation of 0.368 and variable ponds having a standard deviation of 0.269. Though there was a slight difference in standard deviation between the two groupings, Levene's test produced no significant difference in variance between stable and variable ponds.

Comparing the Shannon Index across different environmental characteristics yielded no significant relationships between the observed environmental variability from drone imagery and the on-the-ground vegetation diversity (Figure 6). This result was confirmed using a Bayesian generalized linear mixed model to predict Shannon Index due to variability category. The result showed no credible differences between ponds because of variability category. This was the same for pond area, temperature, NDVI, and plot alignment. Furthermore, the 95% credible intervals included zero for all included coefficients which indicated that there is no strong evidence that these parameters significantly influence the distribution of Shannon Index at these sites.

Though there was no significant difference between the variability and plot alignment in Shannon Index, there were slight correlations between the percent cover of grasses and Shannon Index as well as the percent cover of forbs and Shannon Index. Stable plots tended to have lower shrub percent cover (15.4%) but larger forb percent cover (33.4%). Variable plots had higher shrub percent cover on average (21.9%) and lower forb coverage (26.2%). The percent cover of graminoids remained similar across categories (51.1% for stable, 51.8% for variable). The plots with downslope alignment tended to have lower forb percent cover (15.5%) but higher shrub percent cover (33.5%), with the opposite being true for upslope plot alignments (21.9% forb and 26.2% shrub). Once again, graminoid percent cover remained similar across plot alignments (51.0% for downslope and 51.9% for upslope). Despite small differences in functional group composition, no significant difference was detected (Figure 7).

Non-metric multidimensional scaling and PERMANOVA of the species composition and abundance data revealed that grouping factors, variability category, and plot alignment were significant ($p = 0.003$, $p = 0.001$) in explaining the species composition data. Between variability categories, the stable ponds had community compositions that did not exist within variable ponds, though most community compositions found in variable ponds were also found in stable ponds (Figure 8). Assigning the grouping variable to plot alignment shows a significant difference in the upslope and downslope community composition, though there is a large area

of overlap between the two. For both grouping factors, the total variance explained by the individual characteristics was relatively low, with the variability category explaining 5.9% ($R^2 = 0.059$) of the variation in the data and plot alignment explaining 4.4% of the variation in the data ($R^2 = 0.044$).

DISCUSSION

Each factor tested for influence on Shannon Index using a Bayesian model did not show a significant relationship, meaning that the null hypothesis failed to be rejected. This result shows that variation, as seen from the drone imagery, is not the sole determinant of biodiversity as measured by the Shannon Index. The analysis of community composition through NMDS did show significant differences in community composition between variable and stable ponds, though the representation of variance in the data was relatively low. Within the NMDS results, there is evidence that there are some community compositions that exist in stable plots that are not present at variable ponds. This is consistent with observations in the field, where more species appeared at stable ponds than at variable ponds. These observations are backed by the total unique species that only existed at stable ponds, being 22, and the unique species that existed only in variable ponds but not stable ponds, being 15. Previous studies of plant species richness between ponds with varying degrees of environmental variation show an opposite effect of environmental heterogeneity being positively associated with species richness (Holtmann, 2019). While the comparisons of Shannon Index and variability categories showed no significance, there are differences in community composition as observed from NMDS. This indicates that while overall biodiversity, when reduced to a single number for each plot, does not vary due to environmental variation, the total community composition of the plot does. Using a more complex analysis of community structure for environments such as beaver ponds may be more representative of the actual species abundances and compositions than a single number.

A similar phenomenon was observed for plot alignment as compared with the community composition using NMDS, where there were significant differences between upslope and downslope community compositions, though the plot alignment described only a small part of the overall data distribution. The absence of significant relationships between the variables modeled in comparison to vegetation biodiversity and functional group composition points to the complex nature of beaver ponds. The significant results found using NMDS as compared to the results of using Shannon Index to evaluate community composition point to the complex nature of beaver ponds. The reduction of the species' abundance and composition to a single value may be a source of loss of the true complexity of these communities. The overall complexity of environmental factors in determining species assemblages is similarly referenced in Oertli et al 2006, where pond size and different environmental factors were evaluated for

explanation of variance in species composition (Oertli, 2006). They also found that while multiple environmental factors were significant in describing the variance in macroinvertebrate diversity, the factors were less explanatory for vegetative diversity.

The characterization of beaver ponds through spatial data yielded strong patterns between beaver pond surface area and environmental variables. The decrease in mean temperature and increase in temperature standard deviation as beaver pond size increased is aligned with the thermal properties of larger water bodies compared to smaller water bodies. These trends are aligned with the existing literature on pond size and environmental characteristics. From field observations, it appears that the surface area of ponds is analogous to the depth and general size of ponds. The temperature buffering capacity in the larger beaver ponds may be a source of the smaller standard deviation and lower mean temperature detected from the drone imagery. The moderate negative correlation between beaver pond area and NDVI is likely associated with the proportion of open water (low NDVI values) to healthy vegetation (high NDVI values). Smaller ponds appear to have a higher degree of overhanging vegetation matter compared to the larger ponds. The arrangement of vegetation around the ponds is a likely contributor to the difference in NDVI across pond size.

An additional factor that may contribute to the NDVI and pond area relationship is the higher degree of variation in small ponds, as precipitation events and changes in flow likely have a greater proportional effect on small water bodies as compared to large water bodies. The strong positive linear relationship between temperature mean and temperature standard deviation is likely a result of the strong interactions between pond size and these variables. Research has shown that larger, older beaver ponds tend to have lower mean temperature with greater thermal buffering (Burgher, 2023). The moderate quadratic relationship between mean NDVI and NDVI standard deviation indicates that more extreme mean NDVI values are associated with higher NDVI standard deviation values.

Observations in the field indicate that a mosaic of factors may influence the community composition of beaver pond vegetation, as the difference between plots within and across ponds was quite large. From field data collection, the most obvious other factors which may influence local community composition include small-scale hydrology, beaver activity, and substrate type. Many of the most diverse plots appeared to be near the inlets and outlets of the beaver ponds. These locations tended to be close to running water, the level of which decreased rapidly across the time field sampling was completed and were also quite responsive to precipitation events. The inlets and outlets also appeared to have increased evidence of beaver activity. Often, the interfaces between the inlets and outlets were marked by constructed beaver dams, which had flattened vegetation with evidence of herbivory. As beaver activity has been linked with higher heterogeneity, this may have contributed to some

plots having a more heterogeneous community composition. Further investigation into the relative influence of each of these factors in creating microhabitat variations could yield interesting insights into the drivers of vegetative diversity in beaver ponds.

Throughout this process, it was clear that the complex nature of beaver pond vegetation requires a much broader, more robust sampling process size to characterize vegetative diversity across ponds fully. Depending on plot alignment, there was an opportunity for the community composition to change drastically by moving the quadrat a short distance. Improvements to study design, such as evaluating a larger area for vegetation composition (increasing plot quantity and size) and distributing plots across a wider gradient of environmental variability (more ponds with a wider range of variability), may yield more accurate results. There is also an opportunity to evaluate variation in vegetative communities across a range of beaver ponds with a wider distribution of stability. Future research might include evaluations of the plant communities in areas with recently introduced beaver populations as compared with highly stable communities such as those found in the Gothic Townsite. Accounting for the hydrology of the local area in a more tangible way than through spatial data proxies or through ground-truthing, the observations made from the air may also provide insights into the factors that contribute to beaver pond vegetation composition.

I intend to evaluate aspects of environmental variation and vegetative characteristics further this fall for a senior research thesis at Bates College. Future research will include an evaluation of leaf traits across functional groups for the plots already characterized for biodiversity, which will inform a more detailed analysis of functional diversity across the planes of environmental variation. An expanded spatial data analysis will also be undertaken with the goal of characterizing trends in beaver pond characteristics across a broader spatial and temporal scale. Through examining pond characteristics across years and at a greater spatial scale, I intend to develop a methodology for predicting temperature regimes within ponds using remote sensing data such as surface temperature, slope and proxies for hydrological variables.

ACKNOWLEDGMENTS

I would like to first thank my mentor, Ian Breckheimer, for their continued support throughout this research process. I would also like to thank the members of the RMBL Spatial Ecology Lab, Amanda Henderson, Sophia Henderson, and Abe Luedtke, for their encouragement and input. I appreciate the support I have gotten from the RMBL community, especially the Education Program Coordinators Susan Washko and Rosemary Smith.

FIGURES

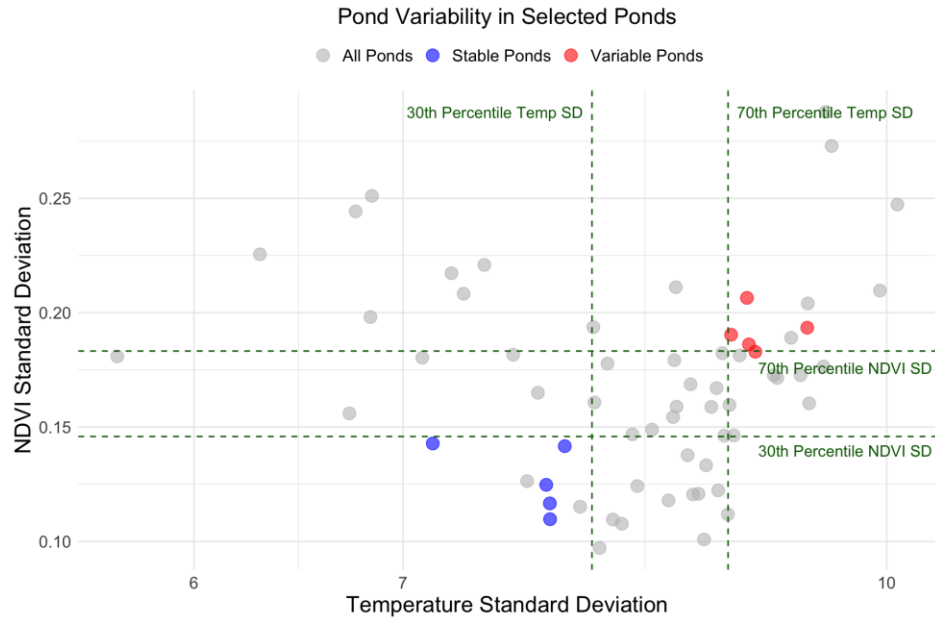


Figure 1: Pond variability across all ponds with the quantiles used to define stable (blue points) and variable (red points) sites.

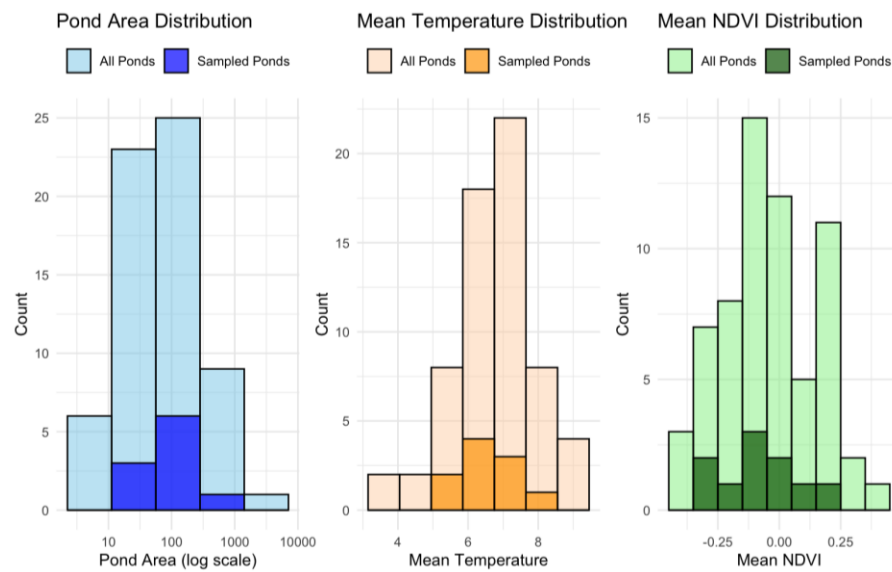


Figure 2: Distributions of pond characteristics, pond area, mean temperature and mean NDVI, for all of the analyzed ponds compared to the ponds selected for on the ground sampling.

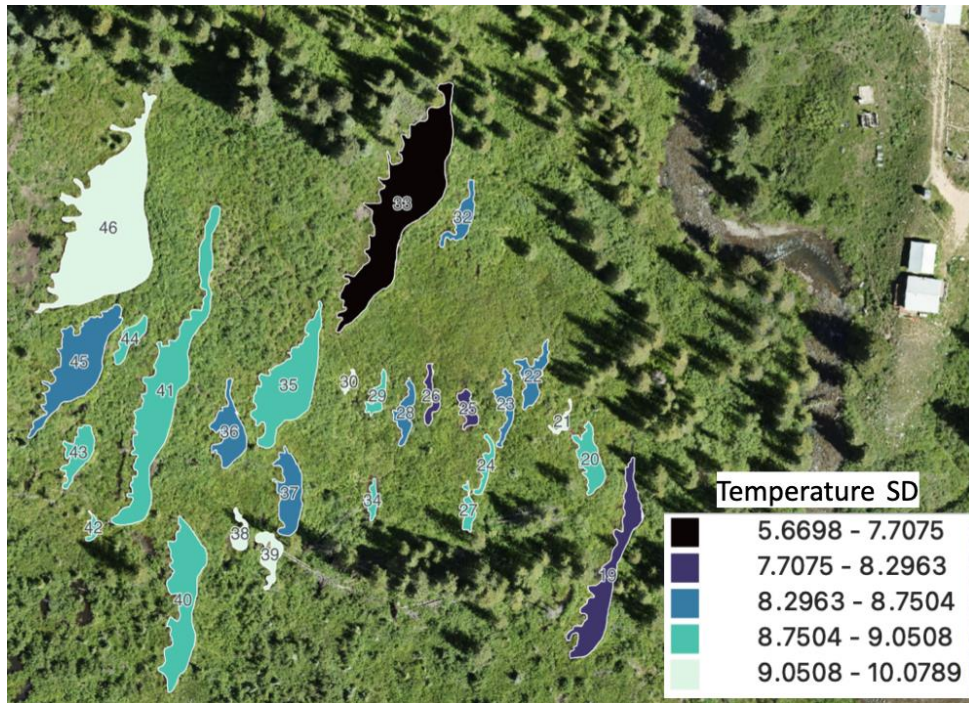


Figure 3: Temperature standard deviation across the Middle Group of ponds with each polygon representing an individual pond and each color representing a temperature standard deviation value.



Figure 4: Beaver ponds with randomized plots from imagery (left), actual sites (middle) and quadrat placement at beaver pond edge (right).

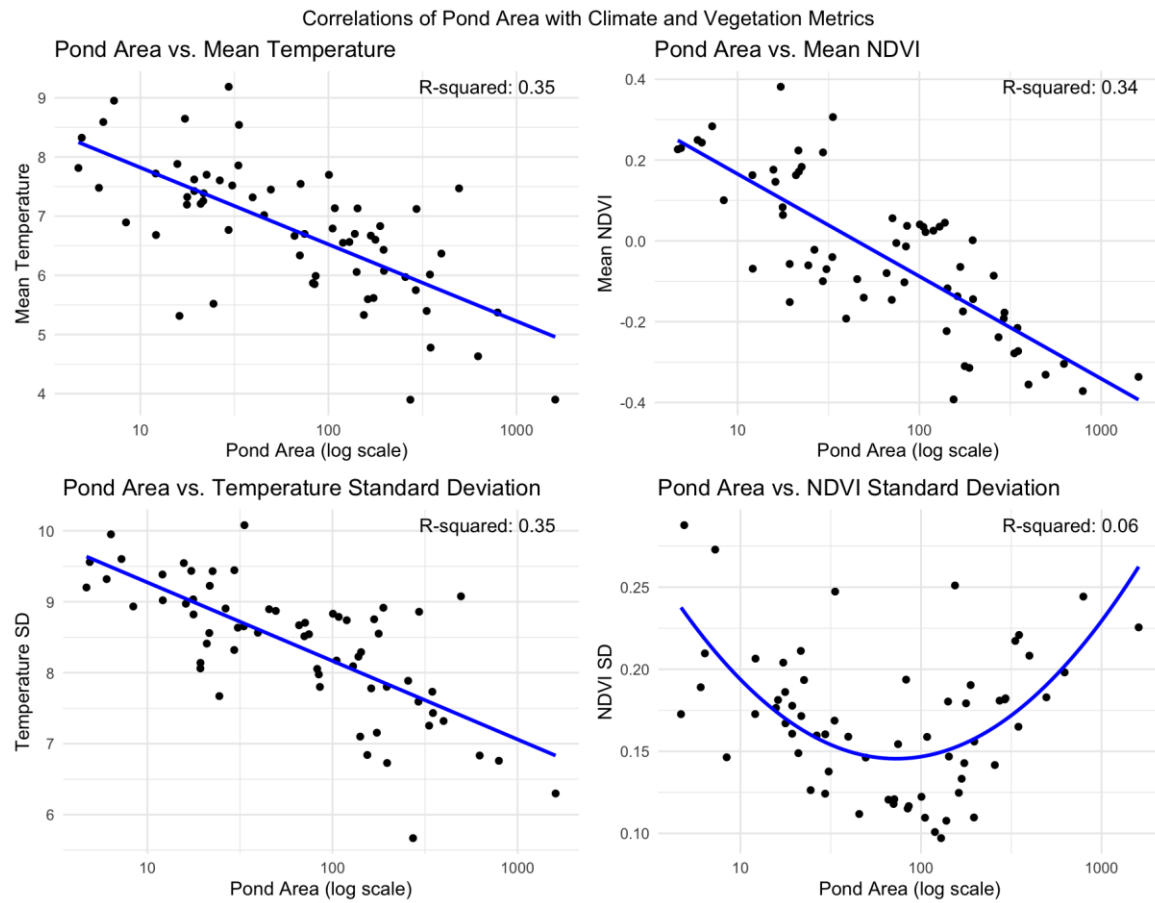


Figure 5: Pond area plotted against climate (temperature) and vegetation (NDVI) metrics.

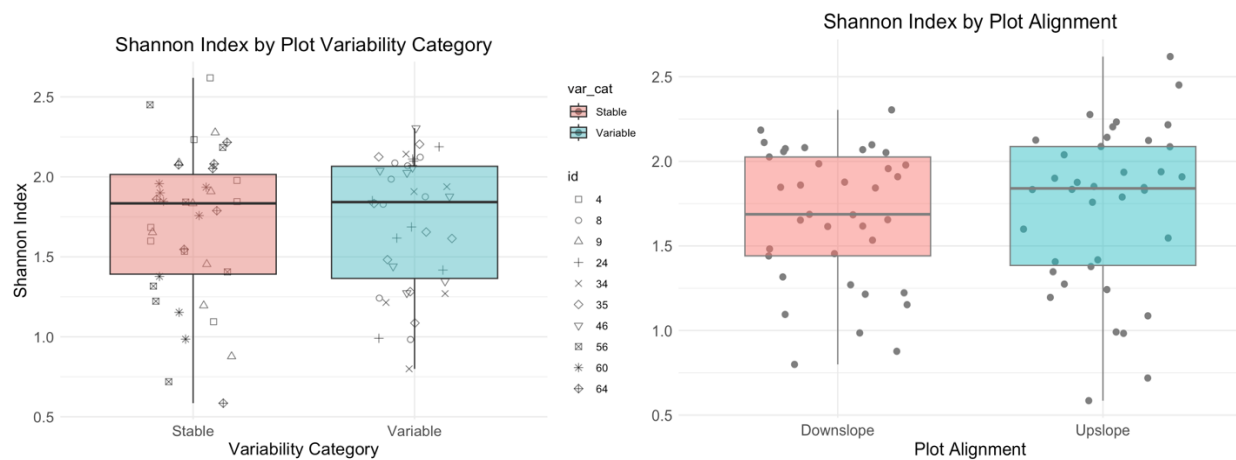


Figure 6: Shannon Index calculated by plot and categorized by variability with individual ponds denoted by point shape (left). Shannon Index calculated by plot and characterized as a downslope or upslope site (right).

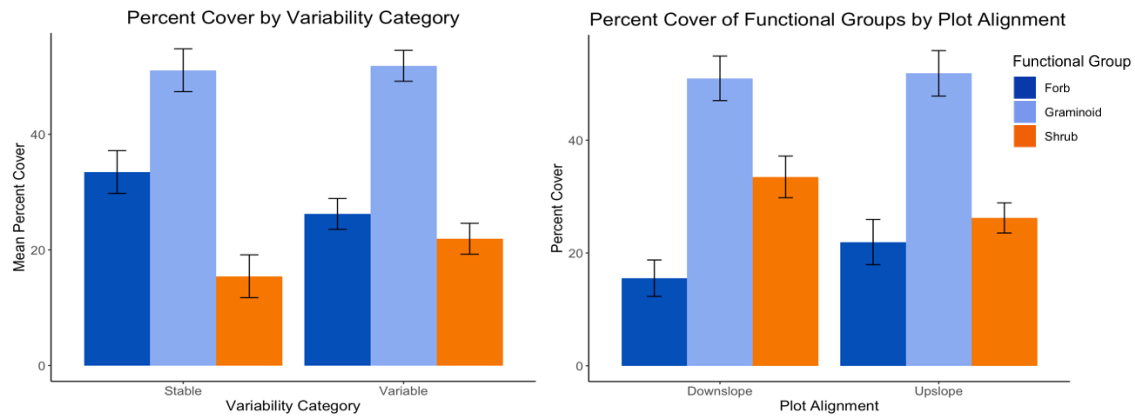


Figure 7: Percent cover by functional group, categorized by variability category (left) and plot alignment (right).

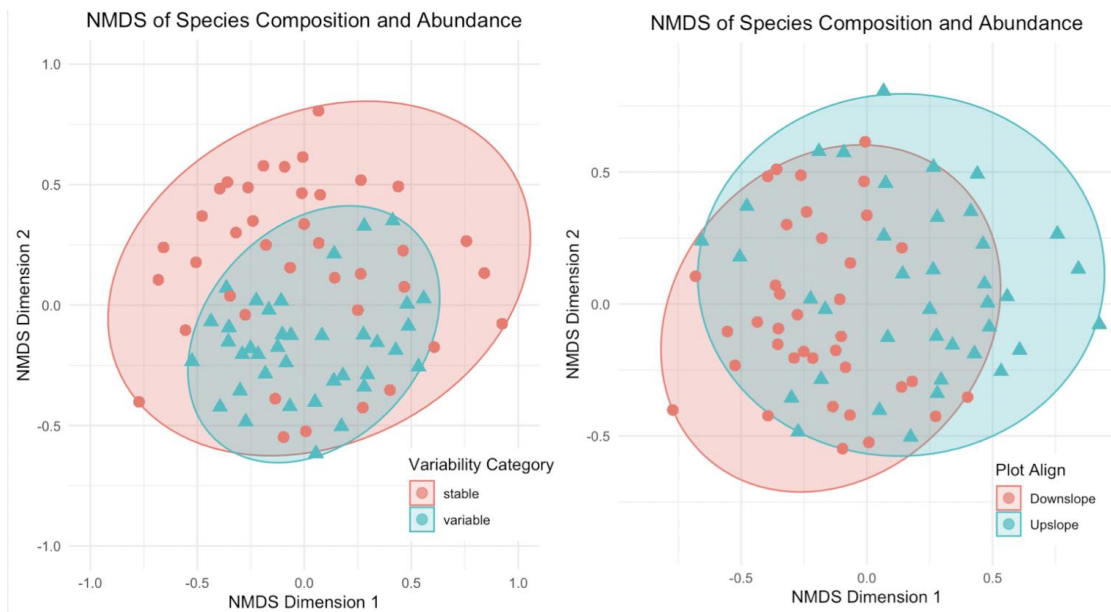
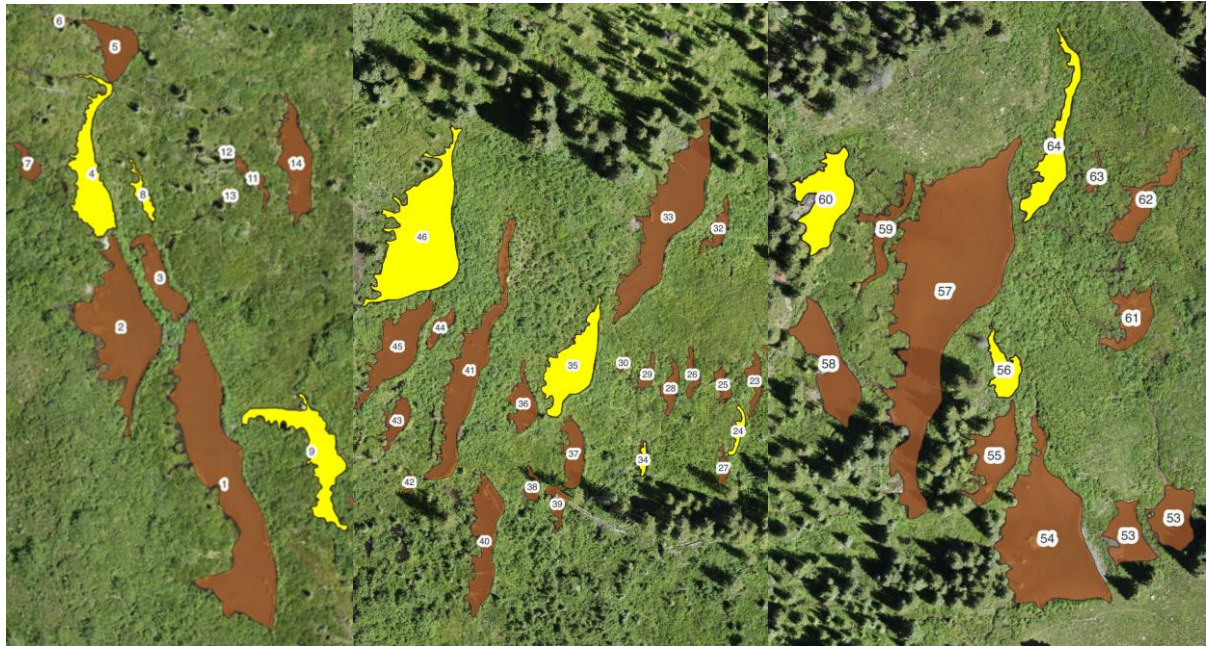


Figure 8: NMDS of species composition and abundance, grouped by variability category (left) and plot alignment (right). Each point is representative of the community composition of an individual plot.

APPENDICES



Appendix 1: Grouping of sites on Gothic Townsite drone imagery.



Appendix 2: Delineated beaver ponds overlaid on Gothic Townsite orthomosaic including South group (left) and Middle group (middle) and North group (right).

REFERENCES

- Baker, B. W., & Hill, E. P. (2003). Beaver (*Castor canadensis*). In G. A. Feldhamer, B. C. Thompson, & J. A. Chapman (Eds.), *Wild mammals of North America: Biology, management, and conservation* (pp. 288-310). Johns Hopkins University Press.
- Bonner, J. L., Anderson, J. T., Rentch, J. S., & Grafton, W. N. (2009). Vegetative composition and community structure associated with beaver ponds in Canaan valley, West Virginia, USA. *Wetlands Ecology and Management*, 17(5), 543–554. <https://doi.org/10.1007/s11273-009-9131-0>
- Brazier, R. E., Puttock, A., Graham, H. A., Auster, R. E., Davies, K. H., & Brown, C. M. L. (2021). Beaver: Nature’s ecosystem engineers. *Wires. Water*, 8(1), e1494. <https://doi.org/10.1002/wat2.1494>
- Burgher, J., Hoza, J., & Piovita-Scott, J. (2023). American beaver (*Castor canadensis*) and freshwater climate resiliency in Washington State.
- Dornelas, M. (2010). Disturbance and change in biodiversity. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1558), 3719–3727. <https://doi.org/10.1098/rstb.2010.0295>
- Dronova, I., Taddeo, S., & Harris, K. (2022). Plant diversity reduces satellite-observed phenological variability in wetlands at a national scale. *Science Advances*, 8(29), eabl8214. <https://doi.org/10.1126/sciadv.abl8214>
- Fraser, R. H., Olthof, I., & Berezanski, D. (2024). Large multi-decade beaver ponding changes in the subarctic Hudson Bay Lowlands, Canada observed using satellite remote sensing. *Environmental Research Letters*, 19(4), 044061. <https://doi.org/10.1088/1748-9326/ad36d6>
- Fairfax E, Small EE. Using remote sensing to assess the impact of beaver damming on riparian evapotranspiration in an arid landscape. *Ecohydrology*. 2018; 11:e1993. <https://doi.org/10.1002/eco.1993>
- Goodrich B, Gabry J, Ali I & Brilleman S. (2024). rstanarm: Bayesian applied regression modeling via Stan. R package version 2.32.1 <https://mc-stan.org/rstanarm>.
- Grime, John, K. Thompson, Roderick Hunt, John Hodgson, Johannes Cornelissen, I. Rorison, G. Hendry, et al. “Integrated Screening Validates Primary Axes of Specialisation in Plants.” *Oikos* 79 (June 1, 1997): 259–81. <https://doi.org/10.2307/3546011>.
- Hill, H., & Ritter, D. (2023). Assessing the Efficacy of Beaver Dam Analogs in Willow Restoration.

- Houlahan, J.E., Keddy, P.A., Makkay, K. *et al.* The effects of adjacent land use on wetland species richness and community composition. *Wetlands* 26, 79–96 (2006).
[https://doi.org/10.1672/0277-5212\(2006\)26\[79:TEOALU\]2.0.CO;2](https://doi.org/10.1672/0277-5212(2006)26[79:TEOALU]2.0.CO;2)
- Law, A., Levanoni, O., Foster, G., Ecke, F., & Willby, N. J. (2019). Are beavers a solution to the freshwater biodiversity crisis? *Diversity and Distributions*, 25(11), 1763–1772.
<https://doi.org/10.1111/ddi.12978>
- Oertli, B., Joye, D. A., Castella, E., Juge, R., Cambin, D., & Lachavanne, J.-B. (2002). Does size matter? The relationship between pond area and biodiversity. *Biological Conservation*, 104(1), 59–70. [https://doi.org/10.1016/S0006-3207\(01\)00154-9](https://doi.org/10.1016/S0006-3207(01)00154-9)
- Oksanen J, Simpson G, Blanchet F, Kindt R, Legendre P, Minchin P, O'Hara R, Solymos, P, Stevens M, Szoecs E, Wagner H, Barbour M, Bedward M, Bolker B, Borcard D, Carvalho G, Chirico M, De Caceres M, Durand S, Evangelista H, FitzJohn R, Friendly M, Furneaux, B, Hannigan G, Hill M, Lahti L, McGlinn D, Ouellette M, Ribeiro Cunha E, Smith T, Stier A, Ter Braak C, Weedon J (2024). *_vegan: Community Ecology Package_*. R package version 2.6-6.1, <https://CRAN.R-project.org/package=vegan>
- Pilliod, D. S., Rohde, A. T., Charnley, S., Davee, R. R., Dunham, J. B., Gosnell, H., Grant, G. E., Hausner, M. B., Huntington, J. L., & Nash, C. (2018). Survey of Beaver-related Restoration Practices in Rangeland Streams of the Western USA. *Environmental Management*, 61(1), 58–68. <https://doi.org/10.1007/s00267-017-0957-6>
- Rakowska, R., & Stachurska-Swakoń, A. (2023). Consequences of the activities of Eurasian beaver on local plants and vegetation cover – an overview. *Environmental & Socio-Economic Studies*, 11(3), 33–42. <https://doi.org/10.2478/enviro-2023-0015>
- Scamardo, J., & Wohl, E. (2020). Sediment storage and shallow groundwater response to beaver dam analogues in the Colorado Front Range, USA. *River Research and Applications*, 36(3), 398–409. <https://doi.org/10.1002/rra.3592>
- Willby, N. J., Law, A., Levanoni, O., Foster, G., & Ecke, F. (2018). Rewilding wetlands: Beaver as agents of within-habitat heterogeneity and the responses of contrasting biota. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 373(1761), 20170444. <https://doi.org/10.1098/rstb.2017.0444>
- Wright, Ian J., Peter B. Reich, Mark Westoby, David D. Ackerly, Zdravko Baruch, Frans Bongers, Jeannine Cavender-Bares, et al. “The Worldwide Leaf Economics Spectrum.” *Nature* 428, no. 6985 (April 2004): 821–27. <https://doi.org/10.1038/nature02403>.