

Moss and Vascular Plant Cover Across Elevational Gradients in a Changing Alpine Climate

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Abstract

Mosses are foundational members of alpine plant communities but are often excluded from vegetation monitoring. In this study, I surveyed moss and vascular plant cover across five alpine ridges near Gothic, Colorado to understand how environmental variables shape moss abundance. I analyzed vegetation composition using data and related moss prevalence to elevation, slope, wetness, and climate trends. Moss presence was low across all sites, with most quadrats containing less than 5% moss cover. Wetness emerged as the strongest predictor of moss prevalence, with slope and elevation also influencing patterns in combination. Moss response to climate change was site-specific: rates of change in growing degree days and snowpack persistence over the past 2-3 decades showed inconsistent effects, with only one site (Crystal) showing a positive relationship between warming and moss prevalence. These findings suggest mosses occupy a narrow and shifting niche in alpine habitats, shaped by fine-scale topography and moisture availability. The patchy, low-cover distributions documented here highlight the need for continued monitoring of mosses in alpine climate change research.

Introduction

Mosses are poikilohydric, nonvascular plants that rely entirely on ambient moisture for physiological function, making them highly responsive to microclimatic changes in temperature and precipitation (Proctor 2001; Weber & Wittmann 2007). Found across nearly all terrestrial ecosystems, from arid deserts to alpine tundra, mosses play vital ecological roles in surface hydrology, soil formation, and habitat structure (Slate et al. 2024). In alpine environments mosses can co-occur with vascular plants in patchy mats within protected microsites such as shaded crevices, beneath boulders, or in shallow soil pockets (Bueno de Mesquita et al. 2017; Weber & Wittmann 2007).

Bryophytes exhibit extensive phenotypic plasticity and notable desiccation tolerance, traits that may buffer them against short-term climate variation (Weber & Wittmann 2007). However, their small size, lack of true roots, and reliance on stable microenvironments can limit dispersal and regeneration under rapid environmental change (Johansson et al. 2016). While microhabitats have historically shielded alpine species from broader climatic trends, there is growing evidence that this buffering is weakening; microclimate conditions, especially soil temperature, are

increasingly tracking regional warming, even in formerly stable microsites (Alexander et al. 2018). This suggests that sheltered habitats may no longer protect mosses from climate change, making them vulnerable to replacement by lower-elevation taxa.

Mosses play a critical role in alpine ecosystem function by regulating soil temperature, moisture, and nutrient cycling. Field manipulations of moss mats and vascular plant litter have shown that moss mats often had a stronger influence on soil temperature, moisture, and nitrogen availability than vascular plant litter (Bruno de Mesquita et al. 2017). Specifically, mosses insulated soils from diurnal and seasonal temperature extremes, maintained higher moisture levels during the growing season, and shaped microbial activity in ways that altered nitrogen dynamics. These effects, in turn, influenced which vascular plant species were able to establish. As such, declines in moss cover could serve not only as indicators of climate change, but also as drivers of shifts in alpine plant community composition (Bueno de Mesquita et al. 2017).

Long-term monitoring at Niwot Ridge in Colorado's Front Range has shown that while vascular plant communities have shifted over 21 years, nonvascular groups such as bryophytes, lichens, and biological soil crusts generally declined or remained stable, with no consistent directional change across most sites. These patterns suggest that nonvascular species may be less responsive to recent environmental change, or that they may be declining in ways not captured by broader vegetation trends (Spasojevic et al. 2013).

To better understand these dynamics, I documented current patterns of alpine moss and vascular plant cover across elevation and climate gradients near Gothic, Colorado. These data provide a baseline for how these plant groups co-occur under present-day conditions, particularly in areas where community shifts may emerge under continued climate change. To guide this research, I asked four key questions: (1) Where are mosses currently present in high alpine environments? (2) Are there climatic or topographic predictors of moss abundance? (3) Is climate warming and drying reducing moss presence in exposed alpine habitats? and (4) If so, could the loss of moss lead to reduced vascular plant cover as well?

Methods

Study Area & Site Selection

This project took place on five exposed alpine ridges north of Gothic, Colorado: Crystal Peak, its neighboring ridge, Treasury Mountain, Cinnamon Mountain, and Gothic Mountain (**Figure 1**). I selected study sites based on three primary criteria: (1) elevation above 3,500 meters, (2) absence of tree cover, and (3) variation in slope, aspect, and substrate within traversable alpine terrain.

Site selection also prioritized proximity and accessibility, as ridges needed to be reachable within a reasonable hike from established trails or 4WD roads to allow for safe and efficient data collection during the short alpine growing season. Among potential ridges that met elevation and

vegetation criteria, I favored those that were geographically clustered to minimize macroclimatic variation, allowing exploration of topography and microenvironment as potential drivers of moss abundance.

Field Sampling Protocol

I walked elevational transects along each focal ridge to systematically survey for moss presence and abundance. Each transect spanned an elevational range of approximately 127 to 447 meters, with quadrats placed every 15–30 meters depending on terrain and moss visibility. I preferentially placed quadrats where moss was visible, though fully moss-dominated patches were rare; most quadrats contained less than 5% moss cover, and over a third had less than 1%, even with presence-biased quadrat placement. This design was motivated by the patchy, limited nature of alpine moss cover in the study region, and although it may overestimate overall moss cover in these environments, it allows for documentation of moss occurrence where it exists at present. Specific quadrat placement was adjusted slightly (within 3–5 meters of the transect line) as needed to maintain safety and continuity in steep or rugged terrain. In total, transects included 10 to 19 quadrats each, with elevation ranges from 3,548 m to 4,042 m depending on the site (**Table 1**).

Table 1. Moss Sampling effort and elevational range by site Summary of quadrats sampled per site, with elevational ranges and percent of quadrats with minimal moss cover. Presence-biased sampling was used to identify areas with moss in exposed alpine ridges

Site	Quadrats Sampled	Min Elevation (m)	Max Elevation (m)	Elevational Range	Mean % Moss Cover
Cinnamon	11	3581	3732	151	2.05
Crystal	22	3669	3813	144	2.29
Gothic	19	3548	3834	286	2.62
Treasury	19	3595	4042	447	3.66

At each quadrat, I used the Gaia GPS app to photograph the survey area and record estimated percent cover of mosses, carefully noting any partially hidden patches. I used a Trimble GPS unit to record the quadrat center to sub-meter accuracy (**Figure 1**). While species-level moss identification was beyond the scope of this project, I collected representative samples from some photographed moss patches, labeled them with GPS coordinates, and donated them to the RMBL Herbarium for preservation and future identification. Each sample consisted of a small pinch of moss placed in a labeled coin envelope.

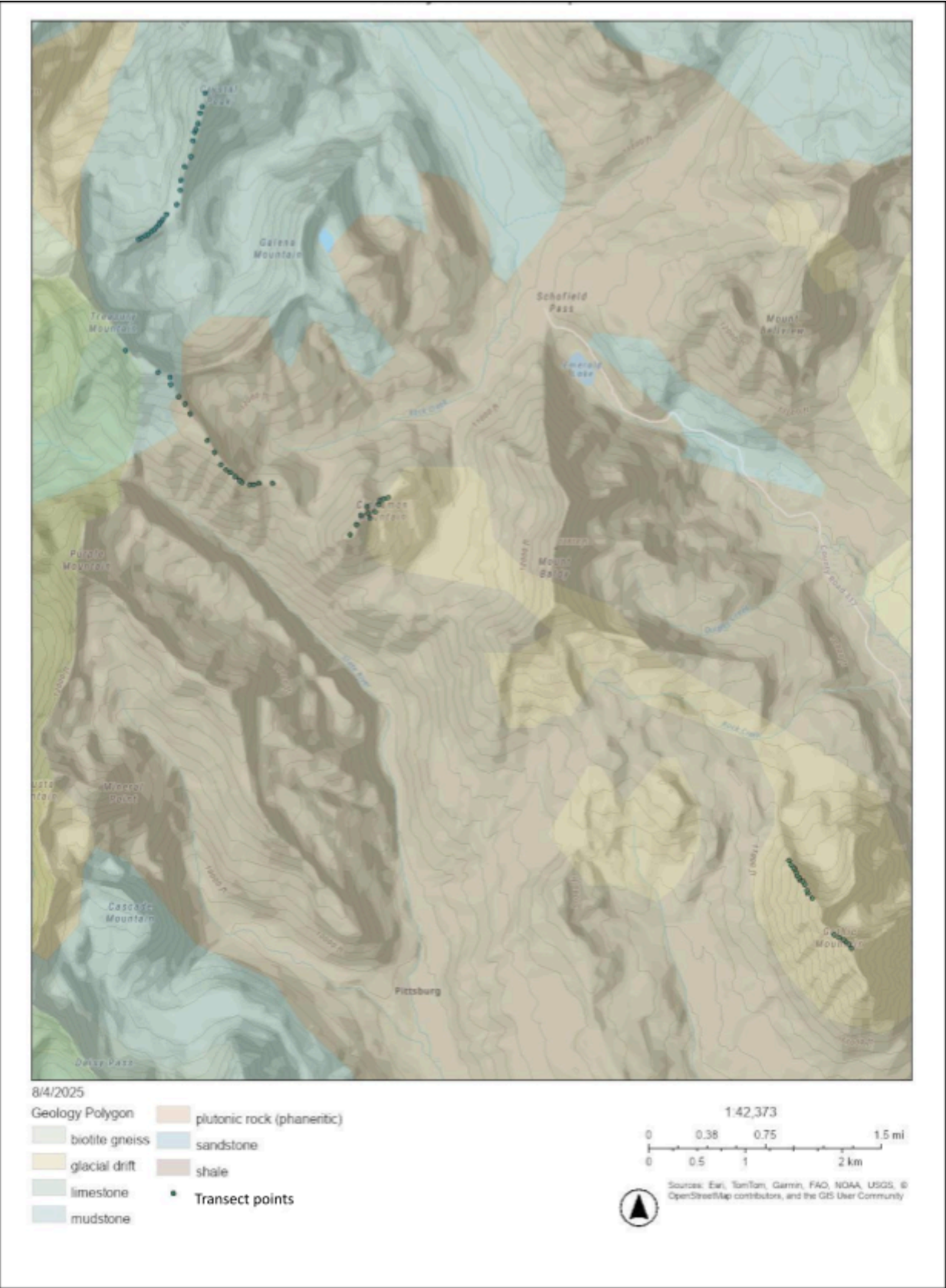


Figure 1. Site map showing transect path and quadrat points.

Estimating moss abundance

To quantify vegetation cover, I used the gridoverlay plugin on gridify.it to apply a 50×50 grid (1 cm² resolution) to each quadrat image, enabling consistent and replicable visual estimation. I classified all vegetation as mosses or vascular plants based on structural characteristics and supporting field notes. For each quadrat, I then calculated percent cover for both groups. To assess relative moss dominance, I derived a composite variable called “moss prevalence,” calculated as:

$$\text{Moss Prevalence} = (\% \text{ moss cover}) \div (\% \text{ vascular plant cover})$$

This ratio served as a response variable in several analyses and reflects the proportional abundance of mosses relative to vascular plants. To isolate the influence of local microsite variables beyond elevation, I extracted the residuals from a linear model regressing moss prevalence against elevation. These elevation-adjusted values were then visualized against other predictors.

Environmental data

I extracted environmental data for each quadrat based on its GPS coordinates using ArcGIS Online and the RMBL Spatial Data Platform (Release 4). Topographic variables included elevation, slope, and aspect (derived from LiDAR rasters), as well as topographic wetness index from multiscale terrain analysis. Climate data were obtained from gridded projections at spatial resolutions of ~1–30 m. The specific climatic variables I considered included: Snowpack Persistence Day of Year (“R4D001”); GDD Early Season Mean (2002–2021) (“R4D045”); GDD Late Season Mean (2002–2021) (“R4D047”); Snowpack Duration Mean (1993–2022) (“R4D057”) and Multiscale Topographic Wetness Index (“R3D001”).

Among these, I focused on two long-term climate variables: Snowpack Duration Mean and Early Season GDD Mean, due to their ecological relevance in alpine systems. Snowpack duration reflects soil moisture availability and length of the growing season, while GDD serves as a proxy for accumulated thermal energy. Because mosses and vascular plants respond differently to these thresholds, they serve as biologically meaningful predictors of community composition. I also included the multiscale topographic wetness index because it captures how landscape position influences water accumulation and drainage, which are critical for poikilohydric species like mosses that rely on ambient moisture. This metric integrates slope and proximity to bodies of water to estimate potential soil moisture patterns, making it a strong proxy for the microhabitat wetness conditions that can shape moss distribution in alpine environments.

To assess the role of climate change specifically, I extracted site-level time series of snowpack persistence (Snowpack Duration – Annual Timeseries (1993–2022) (“R4D003”)) and GDD (Snow-Free Growing Degree-Days, Early Season – Annual Time Series (2002–2022) (“R4D020”)), fitting linear regressions against year to estimate their rates of change over time at each quadrat. The resulting slope coefficients were then used as predictors of moss prevalence. This allowed me to test whether recent rates of climate change are associated with current moss-to-vascular dominance patterns.

Data Analysis

I used multiple linear regression to evaluate the environmental drivers of moss cover. Percent moss cover was modeled as a function of elevation, slope, wetness index, site, and their interactions (**Table 2**). Because elevation has a strong effect on moss prevalence, I first removed that effect by extracting residuals from a moss vs. elevation model. When visualizing data, this allowed me to more clearly show how moss prevalence responded to other variables like slope and wetness by using simple two-dimensional scatterplots. Finally, I tested whether recent climate trends, specifically the rates of change in growing degree days (GDD) and snowpack persistence, were associated with moss abundance by regressing moss-to-vascular plant ratios against quadrat-level climate trend data. I conducted all statistical analyses and data visualization in R (Version 2024.12.0+467).

Table 2. ANOVA results for the moss-to-vascular plant cover ratio, testing the effects of elevation, slope, wetness index, and site, as well as their interactions. Wetness was the strongest predictor ($p < 0.001$), followed by elevation ($p = 0.009$) and slope ($p = 0.023$). Significant two-way interactions included elevation $\times$ slope ($p = 0.025$), elevation $\times$ wetness ($p < 0.001$), elevation $\times$ site ($p = 0.022$), slope $\times$ site ($p = 0.011$), and wetness $\times$ site ($p = 0.004$). The four-way interaction was not significant ($p = 0.317$).

	Df	Sum Sq	Mean Sq	F Value	Pr(>F)
Elevation (m)	1	0.57488	0.57488	7.574	0.0093186
Slope	1	0.42689	0.42689	5.6243	0.0233461
Wetness	1	0.5641	2.56541	33.7994	1.36E-06
Site	3	0.08613	0.02871	0.3783	0.7692416
Elevation (m) : Slope	1	0.41707	0.41707	5.495	0.0248754
Elevation (m) : Wetness	1	1.15855	1.15855	15.2639	0.0004083
Slope: Wetness	1	0.01832	0.01832	0.2413	0.6263136
Elevation : Site	3	0.82599	0.27533	3.6275	0.0222255
Slope : Site	3	0.97504	0.32501	4.2821	0.0112336
Wetness : Site	3	0.22811	0.40937	5.3935	0.003702
Elevation (m): Slope : Wetness	1	0.09569	0.09569	1.2608	0.2691517
Elevation (m) : Slope : Site	3	0.35298	0.11766	1.5502	0.2188534
Elevation (m) : Wetness : Site	3	0.23757	0.07919	1.0433	0.3855201
Slope : Wetness : Site	3	0.20629	0.06876	0.906	0.4480507
Elevation (m) : Slope : Wetness : Site	3	0.27835	0.09278	1.2224	0.3160622
Residuals	35	2.65654	0.0759		

Table 3: ANOVA results for a linear model predicting moss:vascular plant dominance ratios based on site, elevation, and recent climate change trends, specifically the slopes of snowpack duration (slope.dur) and growing degree days (slope.grow)—along with their interactions. Significant predictors included slope.grow ($p < 0.001$), site ($p < 0.001$), and the slope.grow $\times$ site $\times$ elevation interaction ($p < 0.001$), indicating that the effects of increasing growing degree days on moss dominance vary across sites and elevations. Snowpack duration slope (slope.dur) was not a significant predictor in this model.

	Df	Sum Sq.	Mean Sq.	F value	Pr(>F)
Slope. Dur	1	0.1796	0.17958	1.9697	0.1692862
Slope. Grow	1	1.3261	1.32608	14.5449	0.0005331
Site	3	0.6554	0.21846	2.3962	0.0847162
Elevation (m)	1	0.0262	0.02622	0.2876	0.5951637
Slope. Dur : Slope : Grow	1	0.2445	0.2445	2.6817	0.1104672
Slope. Dur : Site	3	0.1739	0.05796	0.6357	0.5970263
Slope. Grow : Site	3	0.1447	0.04822	0.5289	0.6654026
Slope. Dur : Elevation (m)	1	0.0512	0.05123	0.5619	0.458497
Slope. Grow : Elevation (m)	1	0.0226	0.02262	0.2482	0.6214939
Site : Elevation (m)	3	2.9777	0.99255	10.8866	3.37E-05
Slope. Dur : Slope.Grow : Site	3	0.0766	0.02552	0.2799	0.8395171
Slope. Dur : Slope. Grow : Elevation (m)	1	0.0186	0.01858	0.2037	0.6545053
Slope. Dur : Site: Elevation (m)	3	0.2565	0.0855	0.9378	0.432799
Slope. Grow : Site: Elvation (m)	3	2.4923	0.83075	9.112	0.0001354
Slope. Dur : Slope. Grow : Site: Elevation (m)	3	0.2671	0.08903	0.9765	0.4148849
Residuals	35	3.191	0.09117		

Results

Where are mosses currently present in high alpine environments?

Mosses were present at all alpine sites but occurred in sparse, patchy distributions. Even with presence-biased quadrat placement, more than one-third of plots contained less than 1% moss cover, and most had less than 5%, with few exceeding 15%. Mosses were typically found in moist, sheltered microsites, such as shaded rock crevices, beneath vascular plant canopies, or occasionally exposed on rocky surfaces with persistent moisture. When modeled independently, elevation was not a significant predictor of absolute moss cover (**Figure 2A**; $p = 0.671$), suggesting that mosses were not more abundant at higher elevations. In contrast, vascular plant cover declined sharply with elevation (**Figure 2B**), and this decline shifted the moss-to-vascular ratio upward at higher elevations (**Figure 2C**). Accordingly, in a multiple regression model of moss:vascular ratio that included elevation, slope, wetness, and site (**Table 2**), elevation did emerge as a significant predictor ($p = 0.009$).

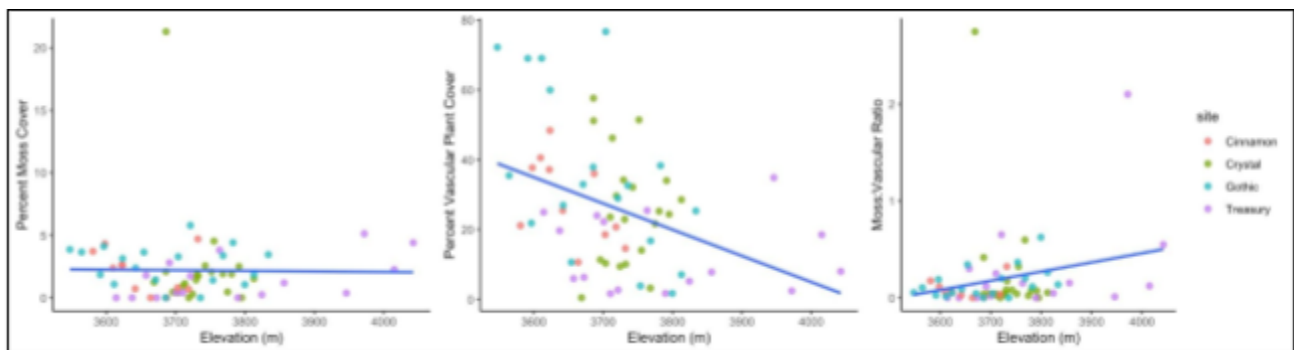


Figure 2: Relationships between elevation and (A) percent moss cover, (B) percent vascular cover and (C) moss-to-vascular plant cover ratio across the four sampled alpine ridges. Each point represents a 1 m² quadrat and is colored by site. While vascular plant cover declines sharply with elevation, moss cover remains consistently low with no strong elevational trend. However, the moss-to-vascular ratio increases slightly with elevation, suggesting a potential shift in dominance dynamics at higher elevations where vascular plant cover is reduced.

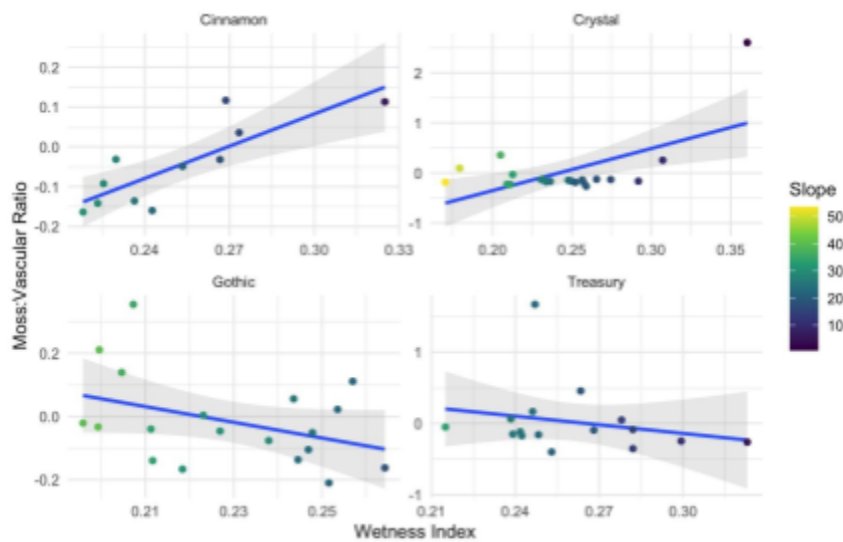


Figure 2: Relationship between wetness index and moss prevalence (expressed as moss:vascular plant cover ratio) across four alpine sites. Each point represents a 1 m² quadrat, with color indicating slope (darker hues = gentler terrain). Trend lines show site-specific linear regressions with 95% confidence intervals. At Cinnamon and Crystal, moss dominance increased with higher wetness, while Gothic and Treasury showed weak or slightly negative relationships. These results suggest that mosses are more abundant in wetter microsites, particularly at sites with higher overall moss prevalence.

Are there any climatic or topographic predictors of moss abundance?

Elevation, slope, and wetness each had significant independent effects on moss:vascular plant prevalence (elevation: $p = 0.009$; slope: $p = 0.023$; wetness: $p < 0.001$). Multiple linear regression identified wetness index as the strongest predictor of moss-to-vascular prevalence ratios ($p = 0.0001$). In addition to these main effects, two-way interactions between elevation and slope ($p =$

0.025) and elevation and wetness ($p < 0.001$) were also significant, suggesting that the influence of slope and moisture on moss prevalence varies with elevation. However, the full three-way interaction between elevation, slope, and wetness was not significant ($p = 0.316$), indicating that while pairs of variables interact meaningfully, adding all three together did not explain additional variation (**Table 2**).

Is climate warming and drying reducing moss presence in exposed alpine habitats?

When moss prevalence was regressed against site-specific rates of change in growing degree days (GDD) and snowpack persistence, only Crystal Ridge showed a significant positive association between increasing GDD and moss dominance (**Figure 3**). No sites

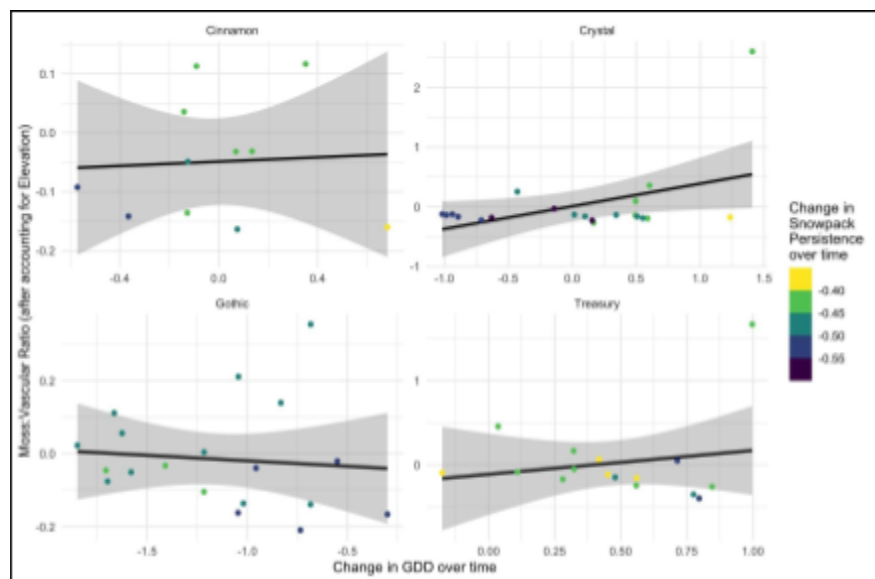


Figure 3: Moss: vascular plant ratio (elevation-adjusted) plotted against changes in growing degree days (GDD) over time across the four alpine sites. Point colors reflect change in snowpack persistence (yellow = greater loss). Only Crystal shows a clear positive trend, suggesting moss dominance may increase with lengthening growing seasons. Other sites showed weak or no relationship.

showed a consistent relationship between snowpack loss and moss prevalence (**Table 3**).

Discussion

Although mosses are critical components of alpine ecosystems, little is known about the environmental factors shaping their current distributions or how these factors might influence future abundance. In this study, I examined moss and vascular plant cover across four high-elevation ridges near Gothic, Colorado to identify the conditions that promote moss dominance and assess their potential sensitivity to climate change. Mosses on the alpine ridges I sampled were sparse, patchy, and mostly limited to sheltered microsites like shaded crevices, exposed rocks, or areas beneath vascular plants. Their presence did not increase with elevation, and most quadrats had less than 5 percent moss cover regardless of altitude. Vascular plant cover, on the other hand, declined significantly with elevation. This suggests that vascular species may be more sensitive to macroclimatic factors such as growing season length or exposure, while mosses may be somewhat buffered by localized microhabitats. These patterns are consistent with existing research on bryophyte ecology, which emphasizes the importance of fine-scale habitat features (Proctor 2001; Weber and Wittmann 2007).

Wetness index was the strongest and most consistent predictor of moss dominance, supporting the idea that moisture availability plays a key role in alpine moss distribution. However, because this index represents topographic position and potential water accumulation rather than direct measurements of soil moisture or precipitation, its ecological meaning may vary depending on the site. Elevation and slope were also significant predictors, but had weaker effects, suggesting that both broader topography and microsite conditions matter. Importantly, the strength and direction of these relationships were not consistent across ridges.

For example, sites with higher wetness index generally had more moss at Crystal and Cinnamon, but not at Gothic or Treasury, where mosses were more common in relatively drier microsites. This variation suggests that other local factors such as snow retention, soil type, or plant competition may also influence moss cover. At Crystal, moss:vascular ratios increased in areas experiencing more rapid warming (greater rates of change in growing degree days). This pattern was unexpected, as some studies report bryophyte declines under warming (Alatalo et al. 2023). It is possible that site-specific factors at Crystal, such as reduced competition from vascular plants or a slightly longer growing season, helped mosses maintain or increase their dominance relative to vascular plants under warming conditions. However, these results reflect present-day patterns in moss dominance and do not address whether these trends will persist over time. Continued monitoring will be essential to determine whether moss gains at Crystal are temporary responses or indicators of a longer-term shift.

Future Directions

To build on these findings, future research should include continuous microclimate monitoring, e.g. using temperature and moisture loggers. This would help capture how daily and seasonal variability influence moss presence beyond what static variables like elevation or slope can explain, and at finer spatial and temporal resolutions than can be projected from downscaled climate data. Expanding sampling across additional mountains, aspects, and years would also allow for the detection of delayed responses in both moss and vascular plant communities to changing environmental conditions. Because mosses are known for their desiccation tolerance and slow recovery dynamics (Proctor 2001), short-term surveys may miss longer-term declines or rebounds.

Further, exploring species-level or trait-based differences among mosses could help explain why certain sites appear more favorable than others. Some taxa may be more resilient to warming or disturbance, which would provide insight into their functional roles in alpine ecosystems. For example, mosses are known to influence soil moisture retention and insulation (Bueno de Mesquita et al. 2017), so understanding their distribution and identity could inform future conservation and monitoring efforts.

Conclusion

This study offers a valuable baseline for monitoring alpine moss and vascular plant communities across high-elevation ridges near Gothic, Colorado. Despite their low overall cover, mosses showed consistent, but sometimes site-specific relationships with environmental factors, particularly those tied to hydrological conditions. The findings point to potential environmental influences on moss patterns, though further research is needed to understand mechanistic causes of differences in moss relationships to environmental factors across sites. Their restricted distribution and sensitivity to microsite conditions suggest mosses may serve as early indicators of ecological change as snowmelt timing and moisture availability shift under ongoing climate change. Continued, fine-scale monitoring will be essential to track where mosses persist and where they begin to disappear in a rapidly changing alpine landscape.

References

Alatalo, Juha M., Annika K. Jägerbrand, and Ulf Molau. “Long-Term Experimental Warming and Nutrient Enhancement Affect Bryophyte and Vascular Plant Cover in a Subarctic Alpine Meadow.” *Plants*, vol. 12, no. 4, 2023, article 806. MDPI, <https://doi.org/10.3390/plants12040806>.

Alexander, Jake M., et al. “Lags in the response of mountain plant communities to climate change.” *Global Change Biology*, vol. 24, no. 2, 2018, pp. 563–579. doi:10.1111/gcb.13976.

Bueno, C. G., et al. “Moss Mediates the Influence of Shrub Species on Soil Properties and Processes in Alpine Tundra.” *PLOS ONE*, vol. 11, no. 10, 2016, e0164143. <https://doi.org/10.1371/journal.pone.0164143>.

Bueno de Mesquita, Clifton P., et al. “Plant colonization of moss-dominated soils in the alpine: Microbial and biogeochemical implications.” *Soil Biology and Biochemistry*, vol. 111, 2017, pp. 135–142. <https://doi.org/10.1016/j.soilbio.2017.04.008>.

Jägerbrand, A.K., et al. “Bryophytes as bioindicators of air pollution and climate change in the Polar Regions.” *Environmental Pollution*, vol. 266, part 2, 2020, article 115991 .

Johansson, Victor, et al. “Air Humidity Thresholds Trigger Active Moss Spore Release to Extend Dispersal in Space and Time.” *Functional Ecology*, vol. 30, no. 7, 2016, pp. 1196–1204. <https://doi.org/10.1111/1365-2435.12607>.

Rydgren, Knut, et al. “Air Humidity Thresholds Trigger Active Moss Spore Release to Extend Dispersal in Space and Time.” *Functional Ecology*, vol. 37, no. 5, 2023, pp. 1139–1151. <https://doi.org/10.1111/1365-2435.14258>.

Schuchardt, Margaret A., et al. “Climate and Species Traits Shape Responses of Alpine Flora in the US Rocky Mountains to a Changing World.” *Global Change Biology*, vol. 29, no. 23, 2023, pp. 6803–6820. <https://doi.org/10.1111/gcb.16854>.

Gril, Eva, et al. “The Affinity of Vascular Plants and Bryophytes to Forest Microclimate Buffering.” *Journal of Ecology*, vol. 113, 2024, pp. 22–38. <https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2745.14425>

Lamprecht, A., Semenchuk, P.R., Steinbauer, K., Winkler, M. and Pauli, H. (2018), Climate change leads to accelerated transformation of high-elevation vegetation in the central Alps. *New Phytol*, 220: 447-459. <https://doi.org/10.1111/nph.15290>

Lesica, Peter. "Arctic-alpine plants decline over two decades in Glacier National Park, Montana, USA." *Arctic, Antarctic, and Alpine Research* 46.2 (2014): 327-332.
<https://www.tandfonline.com/doi/full/10.1657/1938-4246-46.2.327>

Proctor, M.C.F. "The Bryophyte Paradox: Tolerance of Desiccation, Evaporation Control, and the Challenges of Microhabitat." *International Journal of Plant Sciences*, 2001.
<http://www.bioone.org/doi/abs/10.1639/0007-2745%282007%29110%5B595%3ADIBAR%5D2.0.CO%3B2>

Slate, Megan L., et al. "Impact of Changing Climate on Bryophyte Contributions to Terrestrial Water, Carbon, and Nitrogen Cycles." *New Phytologist*, vol. 241, no. 3, 2024, pp. 753–768, <https://onlinelibrary.wiley.com/doi/abs/10.1111/nph.19772>

Spasojevic, Marko J., et al. "Changes in Alpine Vegetation over 21 Years: Are Patterns across a Heterogeneous Landscape Consistent with Predictions?" *Ecosphere*, vol. 4, no. 9, 2013, p. 117. <https://doi.org/10.1890/ES13-00133.1>.

Weber, William A., and Ronald C. Wittmann. *Bryophytes of Colorado: Mosses, Liverworts, and Hornworts*. 2nd ed., University Press of Colorado, 2007

Spatial Metadata:

1. Topographic Slope

Breckheimer, Ian. 1 m Resolution Topographic Slope for the Upper Gunnison Basin Derived from 2015 and 2019 LiDAR Data. Rocky Mountain Biological Laboratory Spatial Data Platform,

<https://www.rmbl.org/scientists/resources/data-catalog/data-catalog-entry/?catalog-id=94>.

Accessed 7 Aug. 2025.

2. Westness (Aspect)

Breckheimer, Ian. 1 m Resolution Topographic Aspect “Westness” for the Upper Gunnison Basin Derived from 2015 and 2019 LiDAR Data. Rocky Mountain Biological Laboratory Spatial Data Platform,

<https://www.rmbl.org/scientists/resources/data-catalog/data-catalog-entry/?catalog-id=93>.

Accessed 7 Aug. 2025.

3. Southness (Aspect)

Breckheimer, Ian. 1 m Resolution Topographic Aspect “Southness” for the Upper Gunnison Basin Derived from 2015 and 2019 LiDAR Data. Rocky Mountain Biological Laboratory Spatial Data Platform,

<https://www.rmbl.org/scientists/resources/data-catalog/data-catalog-entry/?catalog-id=92>.

Accessed 7 Aug. 2025.

4. Wetness Index

Breckheimer, Ian. 1 m Resolution Multiscale Height-Above-Stream Wetness Index for the Upper Gunnison Domain. Rocky Mountain Biological Laboratory Spatial Data Platform,

<https://www.rmbl.org/scientists/resources/data-catalog/data-catalog-entry/?catalog-id=102>.

Accessed 7 Aug. 2025.

5. Snow-Free Growing Degree-Days – Early Season Mean (2002–2021)

Breckheimer, Ian. Snow-Free Growing Degree-Days Early Season Mean (2002–2021)

“R4D045”. Rocky Mountain Biological Laboratory Spatial Data Platform,

<https://www.rmbl.org/scientists/resources/data-catalog/data-catalog-entry/?catalog-id=272>.

Accessed 7 Aug. 2025.

6. Snow-Free Growing Degree-Days – Late Season Mean (2002–2021)

Breckheimer, Ian. Snow-Free Growing Degree-Days Late Season Mean (2002–2021) “R4D047”.

Rocky Mountain Biological Laboratory Spatial Data Platform,

<https://www.rmbl.org/scientists/resources/data-catalog/data-catalog-entry/?catalog-id=274>.

Accessed 7 Aug. 2025.

7. Snowpack Duration Mean (1993–2022)

Breckheimer, Ian. Snowpack Duration Mean (Water Year 1993–2022) “R4D057”. Rocky Mountain Biological Laboratory Spatial Data Platform,

<https://www.rmbl.org/scientists/resources/data-catalog/data-catalog-entry/?catalog-id=284>.
Accessed 7 Aug. 2025.

8. Snowpack Persistence Day of Year – Yearly Timeseries

Breckheimer, Ian. Snowpack Persistence Day of Year Yearly Timeseries “R4D001”. Rocky Mountain Biological Laboratory Spatial Data Platform,
<https://www.rmbl.org/scientists/resources/data-catalog/data-catalog-entry/?catalog-id=228>.
Accessed 7 Aug. 2025.

9. Snow-Free Growing Degree-Days Early Season – Annual Timeseries
(2002–2022)

Breckheimer, Ian. Snow-Free Growing Degree-Days Early Season Timeseries “R4D020”. Rocky Mountain Biological Laboratory Spatial Data Platform,
<https://www.rmbl.org/scientists/resources/data-catalog/data-catalog-entry/?catalog-id=247>.
Accessed 7 Aug. 2025.

10. Snowpack Duration – Annual Timeseries (1993–2022)

Breckheimer, Ian. Snowpack Duration Yearly Timeseries “R4D003”. Rocky Mountain Biological Laboratory Spatial Data Platform,
<https://www.rmbl.org/scientists/resources/data-catalog/data-catalog-entry/?catalog-id=230>.
Accessed 7 Aug. 2025.