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RESEARCH ARTICLE

Recreational trails reduce lichen and bryophyte diversity and the occurrence of rare species

Jesse E. D. Miller[1] | **John Villella**[2] | **David Kofranek**[3] | **Jason Clark**[2]

[1]The Evergreen State College, Olympia, Washington, USA

[2]Siskiyou Biosurvey, LLC, Eagle Point, Oregon, USA

[3]David Kofranek Botany, LLC, Eugene, Oregon, USA

Correspondence
Jesse E. D. Miller
Email: kawriver@gmail.com

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Abstract

1. Increasing recreational use of natural areas may pose a threat to biodiversity, particularly in sensitive high-elevation ecosystems. Lichens and bryophytes (collectively termed cryptogams here) contribute substantially to biodiversity in almost all terrestrial ecosystems, but their response to disturbance from recreation has rarely been studied.
2. We inventoried lichen and bryophyte communities and analysed impacts of disturbance and environmental variables at four study areas in Mount Rainier National Park, Washington, USA. The study areas ranged from low-elevation, wet temperate forests to alpine environments and adjacent subalpine forests.
3. A total of 77 liverwort taxa, 203 lichen taxa, and 195 moss taxa were found across all study areas, for a total of 475 cryptogam taxa. We found that cryptogam richness increased with increasing distance from trails across all study sites, even as far as 75 m from trails.
4. Negative effects of visitor use on cryptogam communities appeared to be particularly pronounced in alpine areas. Rare cryptogam occurrences were associated with less trampled, wetter, and rockier sites in the alpine zone; we did not identify any drivers of rare cryptogam occurrences in forest areas.
5. *Synthesis and applications*. Our results highlight that ecological impacts of recreational use may extend great distances from trails and other heavily used areas. Additional efforts by land managers to prevent visitors from walking off-trail in heavily visited areas could help conserve lichen and bryophyte diversity.

KEYWORDS
biodiversity, bryophytes, conservation, cryptogams, disturbance, lichens, recreation, trails

1 | INTRODUCTION

Recreational use of natural areas can cause substantial disturbance to ecosystems, particularly in low-productivity ecosystems such as alpine areas, which have experienced increasing visitor use in recent years (Barros et al., 2020; Rice & Pan, 2021). Recreational activities can cause a decline in total vegetation cover (Monz, 2002) as well as decreasing the abundance of specialist or endemic species (Billings, 1973). This poses a challenge for land managers, who are often tasked with facilitating recreation access while minimizing disturbance to sensitive ecosystems (Kuba et al., 2018). While there have been many studies of visitor use impacts on vegetation (e.g., Pescott & Stewart, 2014), there are fewer studies that pertain to non-vascular organisms such as lichens and bryophytes, despite the important roles that they play in ecosystems (Crisfield et al., 2012; Jägerbrand & Alatalo, 2015; Rawat et al., 2021). Without a clear understanding of how lichens and bryophytes respond to recreational impacts, it is difficult for land managers to make informed decisions for managing visitor use while conserving biodiversity.

Cryptogams, used here as a collective term for lichens and bryophytes, contribute substantially to biodiversity in alpine and arctic regions of the world, in part because their poikilohydric, non-vascular life histories make them able to withstand conditions that are too harsh for most vascular plants. Arctic-alpine cryptogam taxa have long been recognized as a relatively rare and important component of biodiversity in the temperate world (Ellis & Yahr, 2011; Matveyeva & Chernov, 2019). However, research into arctic-alpine taxa has been historically limited, and much previous research occurred in an era prior to modern species concepts for lichens and bryophytes. Despite their substantial contributions to biodiversity and ecosystem functions, threats to cryptogam communities remain poorly understood.

The effects of recreational impacts on cryptogams remain incompletely understood. While cryptogams have been commonly reported to have negative responses to trampling from recreational visitors (e.g., Piscová et al., 2023; Runnström et al., 2019), responses may vary with ecological context, and cryptogams may be resilient to trampling disturbance in some cases (Kerbiriou et al., 2008; Olech, 1996; Törn et al., 2006). Many previous studies have focused on experimental trampling, which may not accurately replicate real-world trampling (e.g., Pertierra et al., 2013; Runnström et al., 2019); observational studies of trail-associated trampling have typically studied only areas immediately adjacent to trails (Arnesen, 1999; Rawat et al., 2021; Studlar, 1980). To fully understand visitor use impacts, comparing cryptogam communities along a long gradient of distance from trails may help elucidate the spatial scale at which recreational visitors influence biodiversity.

The degree to which visitor use impacts vary among ecosystems, or even among microclimates within ecosystems, remains unclear. Much research has focused on sensitive alpine areas (e.g., Crisfield et al., 2012; Jägerbrand & Alatalo, 2015; Rawat et al., 2021), but there has been relatively little such research in more productive ecosystems, such as temperate forests. Performing the same assessment protocols in different ecosystems could help elucidate the degree to which cryptogam responses to disturbance are ecosystem-specific. Further, cryptogams are sensitive to the environment at fine scales, but few trampling studies have controlled for potentially confounding environmental variables. Considering the role of the environment may help elucidate the effects of recreational impacts. Degrading effects of visitor use overlie other widespread threats to cryptogams and their ecosystems in the era of global change, and considering how environmental variation affects cryptogams may also yield insights into potential effects of climate change on cryptogam communities.

Here, we explore the effects of recreational visitor impacts and the local environment on the diversity of cryptogams, as well as the occurrence of rare cryptogam species, in Mt. Rainier National Park, Washington, USA. Mt. Rainier National Park is the second-most visited National Park in the Pacific Northwest region of the USA, and degradation of ecosystems imposed by visitor use in the Park has posed a significant challenge to conservation management in recent years. We focus on the composition of entire cryptogam communities, as well as the ecology of rare cryptogam taxa, which we define as taxa that may be at risk of regional extirpation or global extinction. We ask two main research questions: (1) What are the effects of visitor use on the overall cryptogam community and on the occurrence of rare cryptogam species in high-use areas of the Park? And (2) What are the environmental drivers of cryptogam community composition and the occurrence of rare cryptogam species, and how can managers identify habitats of particular importance for cryptogams? We also explored whether randomly located plots are as effective for locating rare cryptogams as 'intuitively controlled' surveys.

2 | MATERIALS AND METHODS

2.1 | Study areas

Mount Rainier (elevation 4390 m) provides unique and important alpine habitat as the highest peak in Washington State and is the fifth highest peak in the 'lower 48' states of the USA. Mount Rainier contains extensive alpine areas, which are particularly important yet poorly studied habitats for cryptogams. The mountain also creates unique climates at lower elevation; some of the wettest forests in the Cascade Range occur at the base of Mount Rainier, resembling coastal rainforests.

We inventoried lichen and bryophyte communities in two distinct and ecologically important ecosystems in Mount Rainier National Park, alpine ecosystems and montane old-growth forests. We focused on two alpine study areas, Sunrise and Paradise, and two forest study areas, Carbon River and Ohanapecosh (Figures 1 and 2; Table 1). Within selected study areas, we deployed multiple sampling methods, described below. Since our goal was to analyse cryptogam communities across a gradient of disturbance, and because the main study area at Ohanapecosh was largely disturbed by its use as a campground, ~50% of the sampling effort for that area was performed in nearby undisturbed forest including the Grove of the Patriarchs and the surrounding area of Cedar Flats. Sampling this area allowed us to assess baseline, undisturbed cryptogam communities for comparison to more disturbed communities.

Work was performed under research and collecting permit MORA-2023-SCI-0009. This study did not require animal ethics approval.

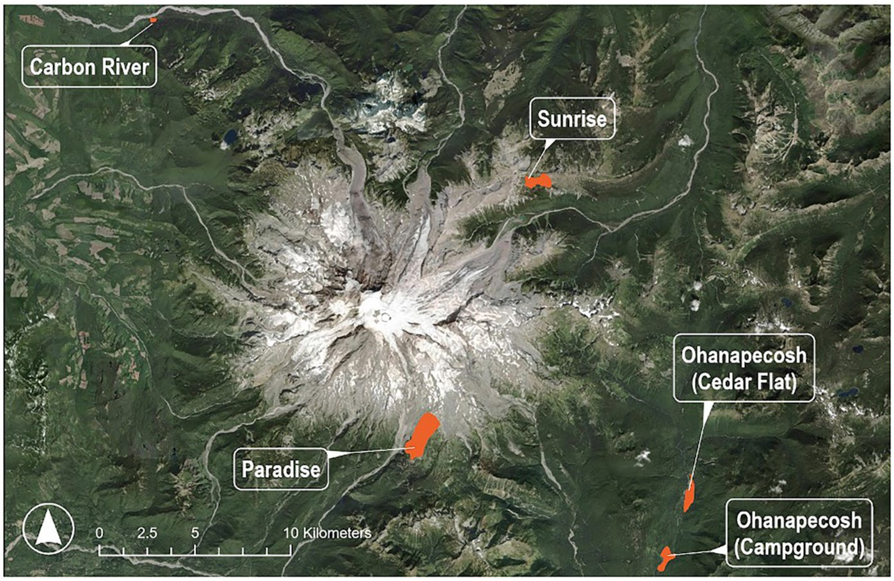

FIGURE 1 Overview map of study areas in Mount Rainier National Park (coordinates 46.85, −121.76).

2.2 | Sampling approach overview

To study drivers of cryptogam communities and their response to visitor use, we used three complementary sampling approaches, which we discuss further below:

1. Belt transects were located at random points along trails, and were used to quantify how far visitor use impacts extend beyond trails themselves in heavy-use corridors in the Park.
2. Randomly located plots documented cryptogam diversity and composition and provided insights into environmental drivers of cryptogam communities.
3. Intuitive-controlled surveys targeted rare species that may not occur in randomly located plots; additional plots were established following the protocol for the random plots when rare cryptogams were encountered (Appendix A).

All field data were collected using the ArcGIS Online Field Maps application (ESRI, 2023). The survey effort in each study area is presented in Table A1. For elements of the protocol that called for random locations, we generated random points for each area and sampling type using GIS software (ESRI, 2023).

2.3 | Belt transects: Assessing visitor use impacts on cryptogams

To assess the relationship between visitor use impacts and cryptogam communities, we established belt transects running perpendicular to official Park trails and campsites at random locations in all four study areas (Figure 3). Transects were 40 m long and were centred on the trail oriented perpendicular to the direction of the trail at the centre of the transect. For transects on trails, a 1-m^2 quadrat was established in the middle of the trail at the centre of the transect. Additional quadrats were established 2.5, 5, 10, and 20 m from the centre of the transect. For transects located at campsites, we used the same protocol except transects were only 20 m long (corresponding to one half of the trail transects, with quadrats at points 0, 2.5, 5, 10, and 20 m from heavily used areas of campsites). The quadrat at 0 was placed on the edge of the high-impact area of the campsite.

In each quadrat, we recorded all cryptogam species present and estimated percent cover for dominant (defined by comprising >5% cover) trees, shrubs, graminoids, and forbs. We also recorded numerous environmental variables (see the full list of variables in the study plot section below) and the distance to the nearest visible official trail or social trail. To characterize hydrologic conditions, we ranked plots on a landscape hydrology index (Table 2), and we also ranked the severity of trampling in each plot on a trampling severity index (Table 3). Photos were taken at all transects and plots that could aid in relocating the exact transect location for future studies.

2.4 | Stratified random plots: Assessing drivers of overall community composition

To assess landscape-scale variation in cryptogam communities and its environmental drivers, we established randomly located study plots within the four study areas. These plots were circular and 405 m^2 in size (~11.35-m radius), following the US Forest Service's common stand exam plot design (USDA, 2015). This allowed our results to be compared with other studies that have used common stand exam plots to characterize lichen communities (e.g., Miller et al., 2018).

The random plots were stratified across different habitat and management histories where appropriate (see Table A1). In all cases,

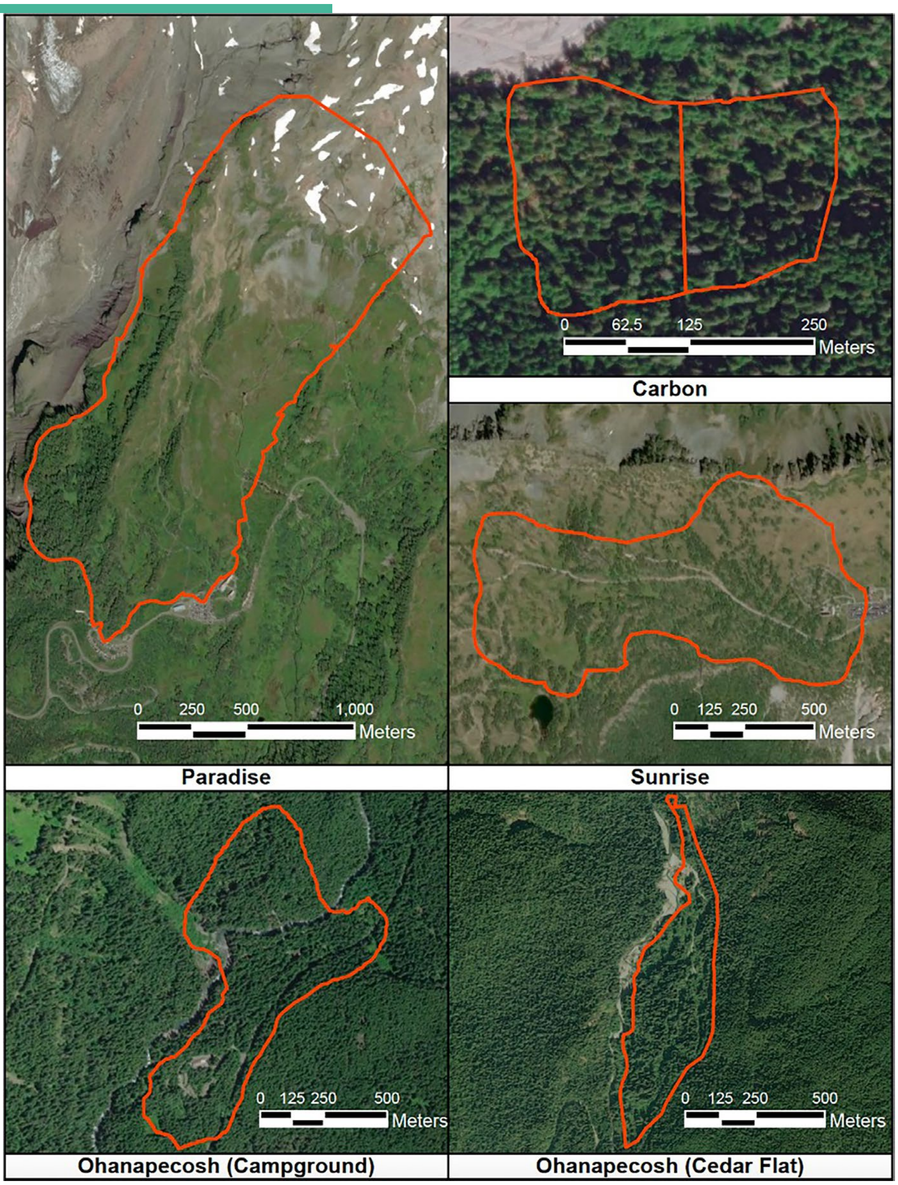

FIGURE 2 Detail map of study areas examined in this study. Ohanapecosh (Cedar Flat) includes the Grove of the Patriarchs.

TABLE 1 Distribution of survey effort across methods and study areas.

Site	Transects	Random plots	Intuitive survey hours	Intuitive plots	Notes
Paradise (~162 hectare)	20	24	24	8	Plots stratified by habitat: Forest, meadows, rocky outcrops, and riparian areas
Sunrise (~73 hectares)	12	14	14	5	Plots stratified by habitat and site history: Forest, meadows, rocky outcrops, riparian areas, and whitebark pine restoration areas
Carbon (~6 hectares)	5	6	6	2	Homogeneous vegetation; no stratification
Ohanapecosh (~108 hectares)[a]	14	16	16	5	Upland and riparian areas were sampled
Total	51	60	60	20	

Note: We sampled cryptogam communities in a total of 2035 quadrats across the three sampling methods.

[a] Includes the 54-hectare Ohanapecosh Campground, the two-hectacre Grove of Patriarchs, and 52 hectare of Cedar Flats.

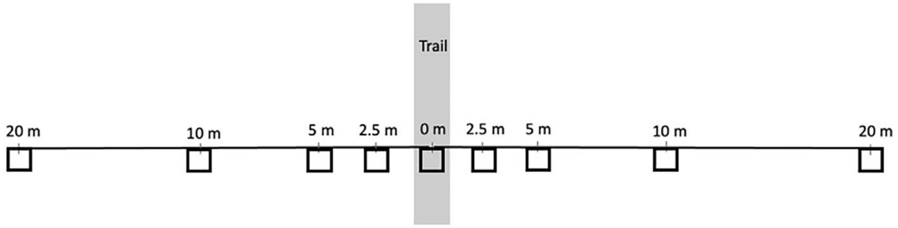

FIGURE 3 Schematic design of belt transects for assessing cryptogam communities adjacent to trails.

TABLE 2 Landscape hydrology index description.

Value	Description
1	Perennial water is present in plot
2	Water is clearly present at least seasonally, with a substantial influence on local ecology
3	Upland plot with some evidence for seasonal water flow
4	Dry, upland plot without any signs of water

TABLE 3 Trampling severity index description.

Value	Description
1	No evidence of trampling
2	Trampling affects a small area of the plot, or ambiguous disturbance where the agent is unknown
3	Moderate trampling: Evidence of trampling (footprints, damage to vegetation, or other clear evidence) in under 50% of plot
4	Heavy trampling: Evidence of trampling (footprints, damage to vegetation, or other clear evidence) in over 50% of plot

random plot centroids were located >32 m from official trails to avoid overlap with the belt transects, since we used the belt transects to assess disturbance effects adjacent to trails, and because the 405-m^2 plots are likely too large to capture fine-scale visitor disturbance impacts.

To allow for comparison between disturbed habitats that are sampled with belt transects, and less disturbed habitats that are sampled with random plots, we established three 1-m^2 quadrats within each plot. The quadrats were located at the plot centre and 10 m from the plot centre at 0 and 180 azimuths (Figure 4). For these quadrats, data were collected following the protocol described in the belt transect protocol above.

Within the entire 405-m^2 area of each study plot, all cryptogam species were recorded. Species that could not be identified in the field were collected for identification in the laboratory. We estimated the abundance of each species using a modified version of the Forest Inventory and Analysis (FIA) lichen plot abundance ranking system (Table 4; Jovan et al., 2020). The original FIA abundance rankings are designed for epiphytes only, and our more flexible modified protocol is designed to allow the abundance of saxicolous and terricolous cryptogams to be tabulated as well.

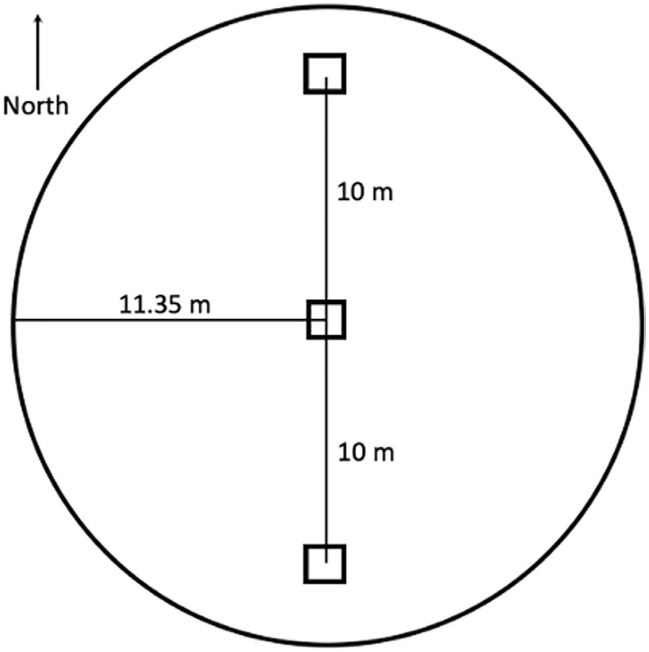

FIGURE 4 Schematic design of 405-m^2 circular plot.

TABLE 4 Modified Forest Inventory and Analysis cryptogam abundance ranking system.

Value	Description
1	1–3 thalli, individuals or colonies present
2	4–10 thalli, individuals or colonies present
3	>10 but <100 thalli, individuals or colonies present
4	>100 thalli, individuals or colonies present
5	>1000 thalli, individuals or colonies present

One photo was taken at each plot from the south edge looking north centred on a temporary marker at plot centre. These provide photo documentation of site conditions and aid in relocating the exact plot locations for future studies.

We recorded the following variables at the plot scale: the identity and abundance rank of each cryptogam species, the identity and cover of each tree, shrub, and herb species that make up more than 5% of total vascular plant cover, total tree cover, total shrub cover, total forb cover, total graminoid cover, bare soil cover, rock cover, average slope, average aspect, the landscape hydrology index (see Table 2, above), the distance to the nearest trial or social trail, and the trampling severity index (see Table 3, above).

2.5 | Intuitive surveys and plots: Assessing drivers of rare species occurrences

To better understand the distribution and ecology of target cryptogams in the study area, we performed intuitive-controlled surveys for populations of rare cryptogams that may be too rare to be detected by random surveys. We defined target cryptogams as taxa that are considered rare by the Park, as well as additional taxa that we determined to be rare taxa of potential conservation concern, many of which were not previously known from the Park (See Appendix A).

The time dedicated to intuitive surveys varied among study areas, with the goal of performing roughly equal survey effort per area in each study area, while accounting for the saturating nature of the species-area relationship (see Table A1). Surveyors searched for target taxa across the landscape, with a focus on areas that appeared to be high-quality habitats, as well as areas where listed cryptogam species had been previously recorded, though exact locations were not available for any of the previously reported populations of listed cryptogams in our study areas (CBH, 2024; CLH, 2024).

When target cryptogams were located or suspected in the field, additional study plots were established following the protocol for the random 405-m^2 plots as described above (Figure 2); these plots were centred on target cryptogam populations. 'Intuitive plots' were also established in some cases to document sites of particularly interesting and diverse cryptogams even if target taxa were not present.

2.6 | Statistical analysis

All data analyses were performed in R version 4.3.1 (R Core Team, 2023).

To explore how the cryptogam community changed with distance from the trail in our four study areas, we used combined quadrat data from belt transects and study plots. We began by performing exploratory analyses and examining scatterplots of focal variables within and among the four study areas. We also used correlation matrices to ensure that predictor variables were not highly correlated (maximum $r = 0.57$ for predictors in the same dataset). To analyse drivers of total cryptogam richness and the cover of each cryptogam type, we used linear mixed models with Gaussian distributions. Distance from the nearest official or social trail was used as the predictor variable and transect ID was included as a random effect. We also ran each model with a quadratic distance term, but these were not significant in all cases and were removed from the models. For all models, we examined model residuals and variable distributions to ensure that model assumptions were met. We used the lme4 package for all mixed models (Bates et al., 2015).

We also used a linear mixed model to explore the relative influence of distance to the trail and other environmental drivers on cryptogam richness in quadrats. We included interactions between distance and slope to test whether visitor use impacts are more localized to the main trail corridor in steeper landscapes, and we tested for similar interactions between rock cover to test whether impacts are less severe in rocky environments. We also compared a version of the model that used topographic heat load (which is derived from slope, aspect, and latitude; McCune & Keon, 2002) in place of slope, and decided whether to use the slope model or the heat load model by comparing Akaike's information criterion (AIC) for the two models (Appendix F). We refined the chosen model by removing non-significant interactions and terms. We used the R^2 function in the performance package to calculate Nakagawa's conditional and marginal R^2 values for linear mixed models, and to calculate Tjur's R^2 for generalized linear models (Lüdecke et al., 2021).

To explore how distance from the trail influences cryptogam community composition, we used a Permanova (permutational multivariate ANOVA) test using Bray–Curtis distance in the vegan package in *R* (Oksanen et al., 2025), with distance from the nearest official or social trail as predictor variables for community composition.

To explore how the cryptogam community responds to the environment at the plot scale, we used several analytic approaches. We analysed random and intuitive plots together for all analyses to increase statistical power and capture the greatest range of variation in environmental conditions and cryptogam communities. Because not all plots analysed were randomly located, inference from these analyses may not apply to the entire landscape. We performed exploratory analyses by examining scatterplots of focal variables within and among the four study areas. We then used linear models to test whether cryptogam richness differed between random and intuitive plots, to test whether the random or intuitive approaches differed in their efficacy for detecting diverse lichen and bryophyte communities. To analyse drivers of total cryptogam richness, we used linear models with environmental variables related to surface cover, plot hydrology, and vegetation structure as predictor variables.

To explore how environmental variables influence cryptogam community composition in plots, we used a Permanova test with numerous environmental variables as predictor variables and visualized species composition using non-metric multidimensional scaling (NMDS) ordinations. The Permanova and NMDS were both performed with a Bray–Curtis distance metric using the vegan package in R (Oksanen et al., 2025).

To explore drivers of target (i.e., rare) species occurrences, we created multispecies distribution models for each major habitat type (alpine and forest areas), where the occurrences of all target species within a habitat type were used as positive values for occurrence, and plots from the same habitat type that did not contain listed species were used as negative values. Specifically, we used generalized linear models with a binomial distribution for the multispecies distribution models. In the species distribution models, environmental variables related to ground cover, vegetation structure and hydrology were used as predictors. We initially included the trampling severity index rather than distance to trail to represent human disturbance in the models, but added distance to trail if trampling severity was not a significant predictor. We did not create species distribution models for individual target species because none occurred frequently enough to provide sufficient inference.

3 | RESULTS

3.1 | Overall diversity

A total of 77 hepatic taxa, 203 lichen taxa, and 195 moss taxa were found across all study areas, for a total of 475 cryptogam taxa (Appendix B). We found 72 occurrences of 24 cryptogam taxa that we identified as target species, which included taxa listed by the Park as rare, as well as additional rare taxa that are not yet on the Park's list. Eight of the hepatics and mosses appear to be rare enough to potentially be considered globally critically imperilled, each with fewer than six known global occurrences. Another nine lichen and bryophyte taxa are rare enough to potentially be considered globally imperilled because each is known from fewer than 20 global occurrences. At the state level, 51 taxa (11% of taxa we found) are known from fewer than six populations in Washington, and another 63 taxa (13% of taxa we found) are known from fewer than 20 populations in Washington (CBH, 2024, CLH, 2024).

3.2 | Effects of trail distance on the cryptogam community

Total cryptogam species richness increased significantly with increasing distance from trails and social trails (hereafter trail distance) in both alpine (Conditional R^2: 0.416, Marginal R2: 0.049, $p<0.001$) and forest (Conditional R^2: 0.301, Marginal R^2: 0.062, $p=0.001$) ecosystems (Figure 5).

Lichen richness increased significantly with increasing trail distance in alpine (Conditional R^2: 0.438, Marginal R^2: 0.021, $p=0.01$) but not in forest ($p=0.6$) ecosystems. Hepatic richness was not significantly affected by trail distance in alpine ecosystems ($p=0.35$), but trail distance had a marginally significant positive relationship with hepatic richness in forest ecosystems (Conditional R^2: 0.215, Marginal R^2: 0.021, $p=0.06$). Moss richness increased with increasing trail distance in both alpine (Conditional R2: 0.354, Marginal R2: 0.053, $p<0.001$) and forest ecosystems (Conditional R^2: 0.231, Marginal R^2: 0.077, $p<0.001$).

In more complex models that accounted for environmental variables, distance to trail interacted with rock cover to affect cryptogam richness in alpine areas (Figure 5; Appendix C, Table 11). Specifically, cryptogam richness increased more strongly with increasing distance from trails in rocky areas than in less rocky areas. We did not include rock cover in models for forests because rock cover was low there. In forests, distance to trail had a positive effect on cryptogam richness in models that accounted for the potentially confounding effects of landscape hydrologic index and topographic heat load (Appendix C, Table 12).

In alpine ecosystems, cryptogam species richness at the quadrat scale was greatest in the wettest places on the landscape; in more humid forests, there was no significant relationship between the landscape hydrologic index and cryptogam richness. In both alpine ecosystems and forests, cryptogam species richness was highest in the topographically coolest microclimates (e.g., sites with low topographic heat load; Figure 6).

Community composition of cryptogams was affected by several environmental variables in a Permanova test: distance to trail, landscape hydrologic index, heat load, rock cover, the trampling severity index, tree cover, shrub cover, and graminoid cover (Table 5). These findings highlight that cryptogam communities are shaped by diverse environmental variables in addition to disturbance caused by Park visitors. However, R^2 values for these relationships were weak (<=0.04 for all predictors in the model); all the predictors we examined explain only a small proportion of variation in cryptogam communities.

3.3 | Environmental drivers of cryptogam richness in random and intuitive plots

In alpine areas, richer cryptogam communities occurred in areas with steeper topographic slopes, in wetter areas, and in less trampled areas (trampling was marginally significant; Table 6). We initially included heat load instead of slope in models of cryptogam richness in plots in alpine areas, but a significant effect of heat load was entirely driven by a single extreme outlier, and the effect of heat load was not significant at the plot scale when the outlier was removed from the model. In this study, heat load appears to have a stronger effect at finer spatial scales (e.g., in quadrats) than at broader scales (e.g., in plots).

In forests, none of the environmental variables we explored were significant predictors of species richness at the plot scale. This suggests that within old-growth forests, cryptogam species richness may be driven more strongly by fine-scale environmental variation (e.g., quadrat scale variation rather than plot-scale variation).

3.4 | Drivers of rare cryptogam occurrences

In alpine areas, target (i.e., rare) species were more likely to occur in plots in wetter, rockier, and less trampled areas (Table 7). There was also a marginally significant, positive effect of graminoid cover on the occurrence of target species. Other predictors we

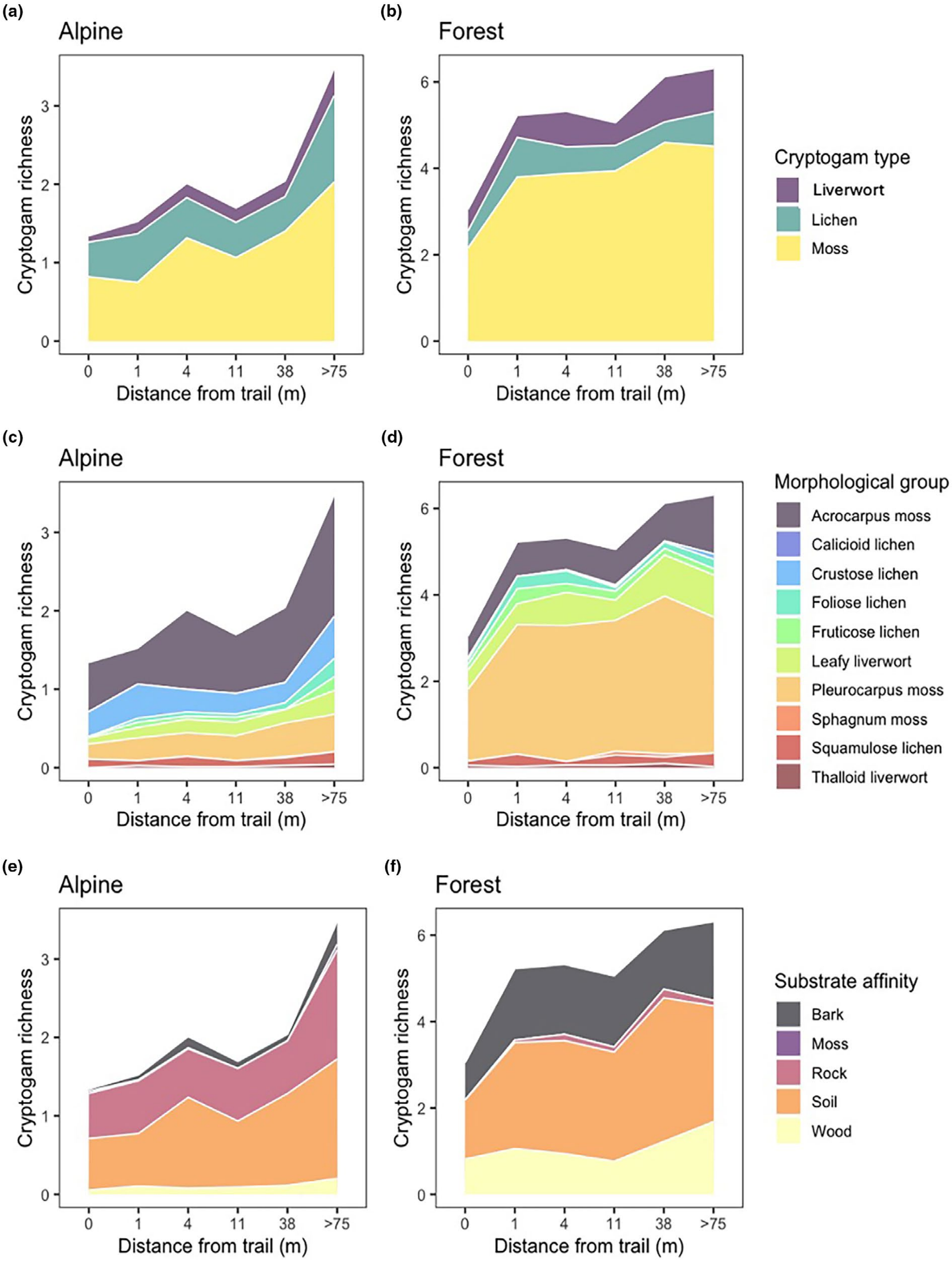

FIGURE 5 Effects of distance from trail on lichen and bryophyte richness in 1 m^2 quadrats. Supplementary plots that show data ranges are included in Appendix E.

investigated, including heat load, forb cover, and shrub cover did not have a significant effect on the occurrence of rare cryptogams in the alpine.

In forest plots, rare cryptogams were more likely to be found farther from trails, and there was a marginally significant, positive effect of shrub cover on rare cryptogam occurrences (Table 8). Other

FIGURE 6 Drivers of cryptogam richness in 1 m^2 quadrats in alpine (left column) and forest (right column) ecosystems; all relationships are significant except (d). Corresponding model results are shown in Appendix C, Tables 11 and 12.

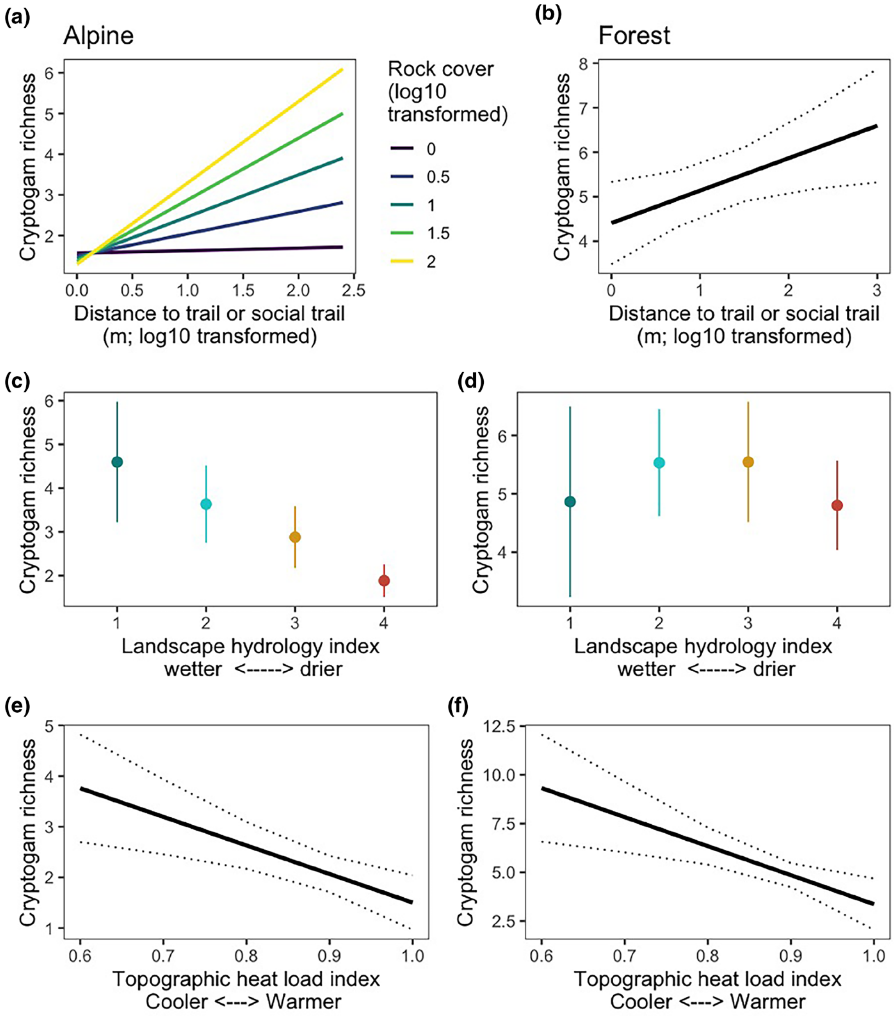

TABLE 5 Model results for Permanova test of drivers of non-vascular species composition in 1 m^2 quadrats.

Variable	R^2 value	*p*-value
Distance to trail	0.01	<0.001
Trampling severity index	0.01	<0.001
Landscape hydrology index	0.03	<0.001
Topographic slope	0.04	<0.001
Rock cover	0.04	<0.001
Shrub cover	0.01	<0.001
Graminoid cover	0.02	<0.001
Tree cover	0.03	<0.001

TABLE 6 Summary of linear model for cryptogam richness in random and intuitive plots in alpine habitat ($R^2 = 0.479$).

Variable	Estimate	SE	*p* value
(Intercept)	19.444	4.885	<0.001
Topographic slope	0.268	0.042	<0.001
Landscape hydrology index	−4.567	1.241	0.001
Trampling severity index	3.006	1.572	0.062

TABLE 7 Multispecies distribution model summary for environmental drivers of target cryptogam occurrences in alpine areas using data from random and intuitive plots (Tjur's R^2: 0.543).

Variable	Estimate	Std. error	*p*-value
(Intercept)	−2.465	1.851	0.183
Landscape hydrology index	−1.105	0.410	0.007
Rock cover	0.057	0.021	0.008
Graminoid cover	0.073	0.038	0.056
Trampling severity index	1.536	0.606	0.011

TABLE 8 Multispecies distribution model summary for environmental drivers of target cryptogam occurrences in forest areas (Tjur's R^2: 0.261).

Variable	Estimate	SE	*p*-value
(Intercept)	−3.903	1.821	0.032
Distance to trail	1.592	0.807	0.049
Shrub Cover	0.049	0.028	0.083

environmental variables we tested did not have a significant effect on rare cryptogam occurrences.

3.5 | Drivers of cryptogam community composition in random and intuitive plots

In alpine areas, slope, the landscape hydrology index, and tree cover were all significant predictors of cryptogam community composition in random and intuitive plots (Permnova $p < 0.001$ for all; Figure 7, upper panel). Plots with high lichen and bryophyte richness appeared to occupy a different part of the ordination space than plots with high graminoid cover. Plots from the Paradise and Sunrise study areas overlap little in ordination space, suggesting there is overall differentiation in the cryptogam communities at these two sites. Plots at Sunrise appear to be associated with drier conditions than those at Paradise; we also observed that unstable substrates that are unsuitable for cryptogams such as pumice gravel were more abundant at Sunrise.

In forests, the landscape hydrology index and topographic slope were significant predictors of cryptogam community composition (Permanova $p < 0.001$ for both; Figure 7, lower panel). Plots that are lichen-rich and bryophyte-rich occupied disparate parts of the ordination space, highlighting the different conditions that lichens and bryophytes need in forests, and probably reflecting the stronger association of bryophytes with wetter conditions.

In alpine areas, intuitive plots had an average richness of 25.5 cryptogam taxa, while random plots had an average richness of 16.2

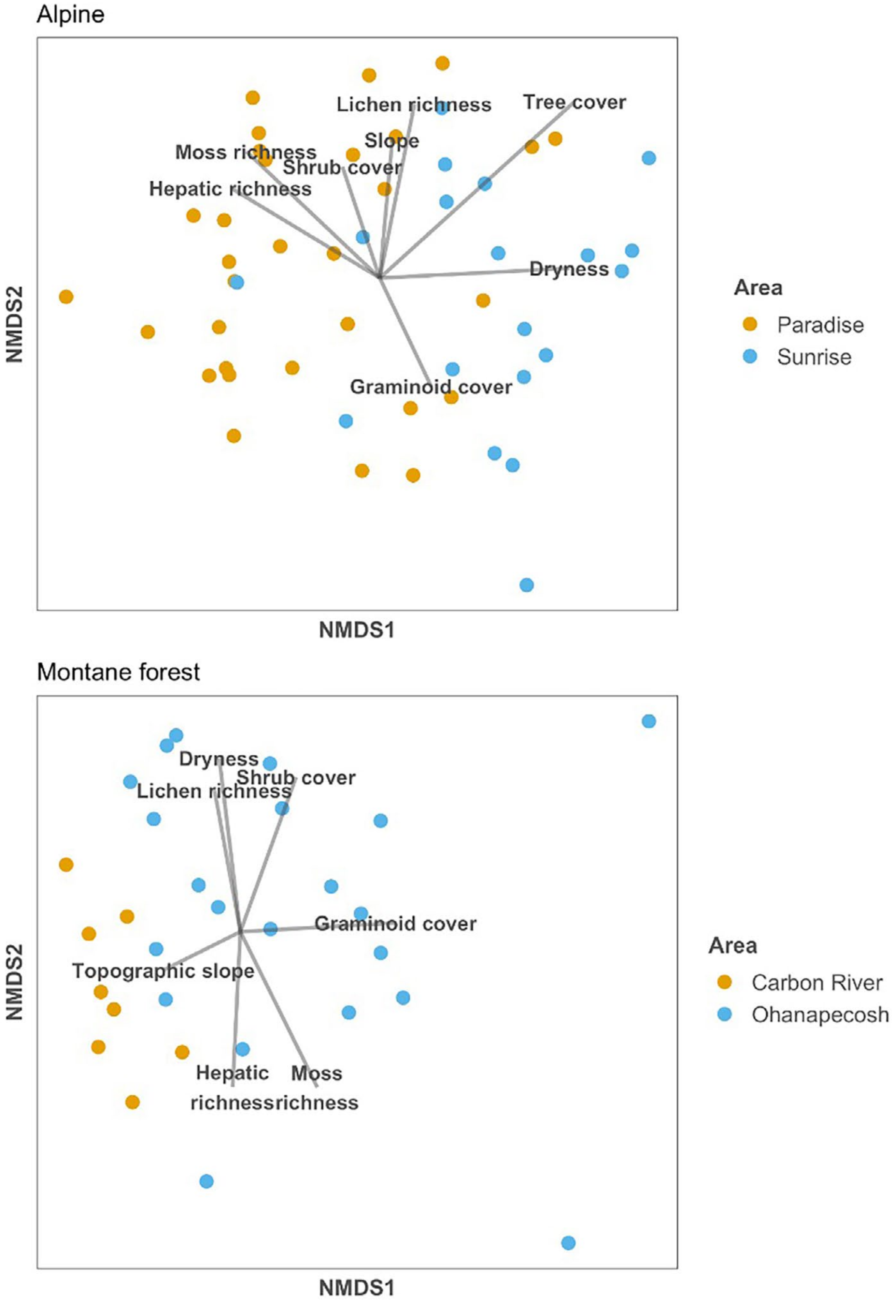

FIGURE 7 Ordination plot showing drivers of cryptogam community composition in forests.

cryptogam taxa. In forest areas, intuitive plots had an average richness of 42 cryptogam taxa, while random plots had an average richness of 33.6 cryptogam taxa. These represent significant differences between richness in intuitive and random plots ($R^2=0.129$, $p=0.01$ for alpine; $R^2=0.17$, $p=0.026$ for forests) and highlight that relatively small areas of the landscape (e.g., habitats sampled in intuitive plots but under-detected by random plots) may contribute disproportionately to cryptogam diversity in the Park. Random sampling does not appear to be as effective as intuitive surveys for capturing the most cryptogam-rich parts of the landscape.

4 | DISCUSSION

Our study highlights that the distribution of lichens and bryophytes is sensitive to both disturbance and environmental conditions at fine spatial scales. Trampling by visitors in heavily used areas has a strong, negative effect on cryptogam species richness, particularly in alpine areas. Cryptogam richness was lowest in and immediately adjacent to trails, in alignment with other previous research on visitor use impacts on alpine lichen and bryophyte communities (Jägerbrand & Alatalo, 2015; Yan et al., 2014). However, our study is unique in exploring visitor use impacts up to a mile or more from trails, and we found that cryptogam richness continued to increase with increasing distance from the trail up to at least 75 m beyond the trail in alpine areas.

Our study is one of the first to explore how visitor use impacts vary among different ecosystems in the same geographic area, and there have been few previous studies of visitor impacts on ecological communities in temperate forests. We found that visitor impacts were strongest in alpine areas, where productivity is lower and regrowth may be slow, but impacts were still substantial in lower elevation forests. In alpine areas, lichen and bryophyte diversity increased incrementally with increasing distance from the trail, up to 75 m or more from the trail. In contrast, while trails were associated with lower lichen and bryophyte diversity in forests, there was only a weak incremental increase in lichen and bryophyte diversity with increasing distance away from trail, once outside of the immediate trail corridor. This may be because visitors do not travel as far off-trail in the dense, vegetated understory of the forests we studied.

We found that visitor use impacts decrease the probability of rare cryptogam occurrences, in addition to reducing overall lichen and bryophyte diversity. Rare lichens and bryophytes are also less likely to occur in areas that have experienced more severe trampling in alpine study areas. Although visible evidence of trampling did not affect rare species occurrences in forests, there was still a trend of rare species being more likely to occur farther from trails. In forests, distance to trail was the only significant predictor of rare lichen and bryophyte occurrences, while environmental variables also affected their occurrences in alpine areas.

In alpine areas we studied, the greatest diversity of lichens and bryophytes occurs in topographically steep, rocky, and wet areas. Lower topographic heat load is associated with greater cryptogam diversity in both alpine areas and forests, though only at fine (e.g., 1 m^2 quadrat) spatial scales. The presence of cool, wet microclimates seems critical to the conservation of lichens and bryophytes in the Park, and these habitats could be vulnerable as climate change continues to have strong warming and drying effects on high-elevation ecosystems (Di Nuzzo et al., 2022). Our finding that microsite-level environmental conditions play a strong role in shaping communities aligns with previous research on both lichen (Ellis, 2012) and bryophyte communities (Monteiro et al., 2023). Topographically steep areas may have particularly high cryptogam richness because they contain more specialized microclimates and because they are probably less affected by human and animal disturbance.

We encountered rare lichens and bryophytes more frequently during ‘intuitive surveys’ than in randomized study plots, and overall lichen and bryophyte diversity was higher in ‘intuitive plots’ (plots that were located based on the presence of rare taxa or apparently diverse communities). These findings highlight that random surveys are unlikely to fully capture occurrences of rare taxa, especially for small organisms such as lichens and bryophytes. While random sampling is an essential tool for establishing average community composition, and for assessing long-term community change, it may not represent all diversity that is present on the landscape.

4.1 | Floristic change

The abundance of rare species that we found highlights the importance of the Park for cryptogam biodiversity. Although we documented many new lichen and bryophyte taxa for the Park, we also did not locate a number of rare taxa that have previously been reported from Mount Rainier, including *Brachydontium olympicum*, *Brachydontium trichodes*, *Bryoxiphium norvegicum*, *Homalia trichomanoides*, *Ptilium crista-castrensis*, and *Tetradontium brownianum*. Because early historical collection records typically cannot be traced to exact locations, mystery surrounds some of these taxa and their current status within the Park. It seems possible that climate change (Alatalo et al., 2020), trail construction (Yan et al., 2014), human trampling impacts (Jägerbrand & Alatalo, 2015), air quality degradation (Oishi, 2019), or other unknown factors could have caused some of the species to be extirpated from the Park, but it is also possible that further surveys in more remote areas of the Park could detect these species.

While several historically present rare mosses of northerly biogeographic affinity were not relocated in the Park, two notable cryptogams of southerly biogeographic affinity were newly discovered in the Park in the course of this study. The moss *Bruchia bolanderi* is new to the state, and the lichen *Tingiopsidium sonomense* is new to the Park. These species both have population centres in subalpine habitats to the south of Mt. Rainier (e.g., in and around California). The disappearance of northerly species and the apparent new arrival of southerly species may be early evidence of thermophilization, a process by which warmer-adapted species are increasing at the expense of colder-adapted species (Gottfried et al., 2012).

Indeed, alpine cryptogam communities are dynamic even at short time scales (Hagenberg et al., 2022), and the changing climate will no doubt affect species and functional group composition (Molau & Alatalo, 1998).

4.2 | Management implications and future research

Minimizing visitor impacts to alpine lichen and bryophyte communities may help them persist. Since we found that the most diverse lichen and bryophyte communities were found in wet, rocky, and steep areas, land managers could route trails away from these habitats to help reduce visitor impacts. Deploying additional infrastructure to protect sensitive habitats, such as fences, railings, and boardwalks, could also be effective. However, maintaining visitor access to natural areas is critical for obtaining public buy-in for conservation, and we believe that visitor use can be facilitated while providing for the wellbeing of sensitive lichens and mosses. Accepting that some degree of visitor impacts will occur in heavily used areas seems reasonable.

Because understanding the effects of visitor use was one major goal of our study, we focused on areas of Mount Rainier National Park that are relatively well-visited. Our research covered only small areas of the Park, and further research could likely uncover many additional lichen and bryophyte taxa that we did not detect. More remote, less travelled areas of the Park, including Elysian Fields and Zurlo Creek, would be good targets for future studies. Continuing to document existing lichen and bryophyte diversity is critical for maintaining biodiversity and understanding the impacts of global change on natural communities.

AUTHOR CONTRIBUTIONS

Jesse Miller designed the study; Jason Clark, Dave Kofranek, and John Villella collected the data; Jesse Miller analysed the data; Jesse Miller led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data are available on the Dryad Digital Repository: https://doi.org/10.5061/dryad.sn02v6xkj (Milller et al., 2026).

ORCID

Jesse E. D. Miller https://orcid.org/0000-0002-2316-779X

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix A. List of lichen and bryophyte target species.

Appendix B. List of all lichen and bryophyte species encountered by study area.

Appendix C. Results from models for lichen and bryophyte diversity.

Appendix D. List of vascular plants encountered by study area.

Appendix E. Figures showing means and variation for cryptogam richness.

Appendix F. AIC tables comparing models for richness in quadrats using topographic slope versus topographic heat load.

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