
Influences of Microhabitat Constraints and Rock-Climbing Disturbance on Cliff-Face Vegetation Communities

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Abstract: *Many researchers report that rock climbing has significant negative effects on cliff biota. Most work on climbing disturbance, however, has not controlled for variation in microsite characteristics when comparing areas with and without climbing presence. Additionally, some researchers do not identify the style or difficulty level of climbing routes sampled or select climbing routes that do not represent current trends in the sport. We solved these problems by sampling climbing areas used by advanced "sport" climbers and quantifying differences in microtopography between climbed and control cliffs. We determined whether differences in vegetation existed between pristine and sport-climbed cliff faces when microsite factors were not controlled. We then determined the relative influence of the presence of climbing, cliff-face microtopography, local physical factors, and regional geography on the richness, abundance, and community composition of cliff-face vascular plants, bryophytes, and lichens. When we did not control for microsite differences among cliffs, our results were consistent with the majority of prior work on impacts of climbing (i.e., sport-climbed cliff faces supported a lower mean richness of vascular plants and bryophytes and significantly different frequencies of individual species when compared with pristine cliff faces). When we investigated the relative influences of microtopography and climbing disturbance, however, the differences in vegetation were not related to climbing disturbance but rather to the selection by sport climbers of cliff faces with microsite characteristics that support less vegetation. Climbed sites had not diverged toward a separate vegetation community; instead, they supported a subset of the species found on pristine cliff faces. Prior management recommendations to restrict development of new climbing routes should be reevaluated based on our results.*

Keywords: cliff vegetation, disturbance, microtopography, Niagara Escarpment, recreation, rock climbing

Influencias de las Reducciones de Microhábitat y de la Perturbación del Escalado de Roca sobre las Comunidades Vegetales en Acantilados

Resumen: *Muchos investigadores reportan que el escalado de rocas tiene efectos negativos significativos sobre la biota de acantilados. Sin embargo, la mayor parte del trabajo sobre perturbación por escalado no ha controlado para variación en las características de microsítios al comparar áreas con y sin escalamiento. Adicionalmente, algunos investigadores no identifican el estilo o nivel de dificultad de las rutas de escalamiento muestreadas o seleccionan rutas que no representan a las tendencias actuales del deporte. Resolvimos estos problemas mediante el muestreo en áreas utilizadas por escaladores "deportivos" avanzados y la cuantificación de diferencias en la microtopografía entre acantilados escalados y control. Determinamos si existían diferencias en la vegetación entre acantilados prístinos y escalados cuando los factores de micrositio no eran controlados. Posteriormente determinamos la influencia relativa de la presencia de escalamiento, la microtopografía del acantilado, los factores físicos locales y de la geografía regional sobre la riqueza, abundancia y composición de la comunidad de plantas vasculares, briofitas y líquenes habitantes en el acantilado. Cuando no controlamos las diferencias de microsítios entre los acantilados, nuestros resultados fueron consistentes con*

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la mayoría de los trabajos previos sobre le impacto del escalamiento (i.e., los acantilados con escalamiento tenían una menor riqueza promedio de plantas vasculares y briofitas así como frecuencias de especies individuales significativamente diferentes en comparación con acantilados prístinos). Sin embargo, cuando investigamos las influencias relativas de la microtopografía y la perturbación por escalamiento, las diferencias en la vegetación no se relacionaron con la perturbación por escalamiento sino con la selección de acantilados con características de micrositios que soportan menos vegetación por los escaladores. Los sitios escalados no habían divergido hacia una comunidad vegetal separada; en vez de ello, soportaban a un subconjunto de especies encontradas en los acantilados prístinos. Con base en nuestros resultados, las recomendaciones previas de restricción del desarrollo de nuevas rutas de escalado deberían ser reevaluadas.

Palabras Clave: escalado de rocas, microtopografía, Niagara Escarpment, perturbación, recreación, vegetación de acantilado

Introduction

Cliff faces are among the few remaining areas on the planet that are largely unchanged by direct human disturbance (Larson et al. 2000). The dramatic increase in the popularity of recreational rock climbing, however, is bringing ever greater numbers of people to this previously untouched habitat (Krajick 1999). Numerous researchers report significant negative effects of rock climbing on the vegetation community on cliffs (e.g., Nuzzo 1996; McMillan & Larson 2002; Rusterholz et al. 2004). Unfortunately, the utility of many of these studies to conservation practice is limited for two reasons: (1) a lack of control for variation in microsite characteristics when comparing areas with and without climbing disturbance and (2) failure to identify the style or difficulty level of climbing routes sampled or selection of climbing routes that do not represent current trends in the sport.

On undisturbed cliffs of the Niagara Escarpment, we recently discovered that vascular plant, bryophyte, and lichen richness and abundance are controlled by local and fine-scale physical factors of the cliff face (Kuntz 2004). Thus, undisturbed sites must precisely match the geological and environmental qualities of climbed sites if differences in vegetation are to be linked conclusively to climbing disturbance. This has not, however, generally been the case. Nuzzo (1995) made no attempt to quantify differences in microtopography between control and climbed sites in Illinois, despite acknowledging the inherent physical variability of cliffs and its potential influence on vegetation density and cover. Rock fracturing was quantified in a subsequent study of climbing impacts (Nuzzo 1996); extreme differences in slope and cliff height, however, existed between disturbance categories, limiting their applicability as controls. Kelly and Larson (1997) and McMillan and Larson (2002) sampled cliffs from a limited geographic region in Ontario to homogenize the influence of climate and excluded cliffs with water seeps, loose rock, or severe overhangs; yet attempts to remove variability at the microtopographic scale were based only on cursory visual inspection. Camp and Knight (1998) removed microtopographic variability on cliffs in Califor-

nia by sampling along a crevice feature but did not control for crevice width, crevice depth, or volume of soil. Light, temperature, humus, and soil nutrients were quantified in a comparison of climbed and unclimbed cliffs in Switzerland (Rusterholz et al. 2004), but underlying differences in microtopography were not examined. Farris (1998) came closest to quantifying the influence of microtopography on cliff vegetation and concluded that cracks, ledges, overhangs, and unbroken rock on cliffs in Wisconsin had unequal probabilities of supporting vegetation. Rock fracturing was coarsely estimated and included in the design of another study of climbing impacts on cliff vegetation in Switzerland, and both rock fracturing and proximity to climbing routes were significant determinants of plant cover, species density, and species richness on the cliff face (Müller et al. 2004). More detailed measures of microtopography, however, may have allowed a clearer interpretation of the factors that drive the divergence in vegetation patterns. Because of inherent differences between sites, experimental studies involving the application of a climbing disturbance to previously unclimbed sites would be better able to determine causality, but the logistics involved in an experimental approach are considerable. Thus, a different comparative design is necessary to control for microhabitat variation.

Another challenge when investigating the impact potential of a particular recreational user group is designing a study that reflects current trends in that activity. The increase in the popularity of rock climbing has resulted in both an increase in frequency of use of existing climbing routes and an increase in the development of new climbing routes. The term *rock climbing*, however, encompasses several distinct sports, including aid climbing, traditional climbing, "sport" climbing, and others (Child 1995), and not all are experiencing new development. Since the 1980s, sport climbing has experienced a rapid expansion throughout Europe, North America, and Southeast Asia (Ficht et al. 1995). On cliffs of the Niagara Escarpment in southern Ontario, Canada, the number of sport-climbing routes has more than doubled over the past decade, whereas no new traditional or aid-climbing areas have been developed (Bracken et al. 1991; Oates

& Bracken 1997; K.L.K., personal observation). Sport-climbing routes follow paths of preinstalled, permanent bolts drilled directly into the rock face to anchor the climber in the event of a fall (Child 1995). In contrast, traditional and aid routes rely on microtopographic features such as crevices in the rock for the placement of safety devices.

The use of bolts by sport climbers has allowed difficult sections of cliff face that lack large ledges and crevices to be climbed in relative safety and has contributed to the recent proliferation of difficult climbing routes. On cliffs of the Niagara Escarpment, only 8 of the 186 new climbing lines established since 1991 were of moderate difficulty (i.e., graded <5.10; 4 were graded 5.9 and 4 were graded 5.8). The rest of the new climbing routes ranged in difficulty from advanced (35 graded 5.10, 66 graded 5.11) to extremely advanced (61 graded 5.12, 13 graded 5.13 and 3 graded 5.14) (Bracken et al. 1991; Oates & Bracken 1997; K.L.K., personal observation).

Thus far, researchers have determined that significant differences in cliff-face vegetation communities exist between heavily climbed cliff faces and cliff faces with no apparent climbing presence, and because of this, management recommendations have been put into place to restrict the development of new climbing routes (e.g., McMillan & Larson 2002; Müller et al. 2004). Results from prior studies, however, should not be used to make predictions about the impact of development of new climbing routes because styles and difficulty levels of routes examined previously do not match the current trends in new-route development detailed above. For example, Kelly and Larson (1997) and McMillan and Larson (2002) examined impacts of climbing on Niagara Escarpment cliff vegetation by sampling traditional climbing routes of moderate difficulty levels (5.7–5.9). These routes receive heavy traffic by climbers; they do not, however, represent the style or difficulty level of >95% of new climbing routes developed on these cliffs (Kuntz 2004). Other researchers sampled climbing routes spanning the range of route difficulties from beginner through advanced (e.g., V. A. Nuzzo, personal communication; H. Rusterholz, personal communication; S. W. Müller, personal communication), which also limits one's ability to interpret the relevance of their results to managing the development of new (difficult) climbing routes.

We overcame the limitations of previous work by separating the presence of climbing from confounding natural environmental factors and by examining the impact of difficult sport-climbing routes on the cliff-face vegetation of the Niagara Escarpment. To this end, we first determined whether differences in the vegetation community existed between sport-climbed and pristine cliff faces when physical differences between disturbance categories were not controlled. We then evaluated the actual influence of sport climbing on the cliff-face vegetation by determining the relative influence of climbing presence, cliff-face

microtopography, local physical factors that influence microclimate, and regional geography on the organization of the cliff-face vegetation community. We also investigated whether climbers are removing vegetation on cliff faces by comparing the sizes of individual microtopographic features supporting and not supporting vegetation on both pristine and sport-climbed cliff faces.

Methods

Study Area

The Niagara Escarpment is a series of dolomitic limestone outcrops that extend from the Bruce Peninsula to the Niagara region in southern Ontario, Canada, and through Michigan, Wisconsin, northern Illinois, and northeastern Iowa, United States. Generally, the Silurian-aged rim is buried by glacial till, but approximately 150 km of exposed, vertical cliff face is present in Ontario (Tovell 1992). To capture regional variation in the effects of sport climbing, we sampled in the three main geographic areas of the Niagara Escarpment in Ontario where sport climbing occurs: Bruce Peninsula (44°55'N, 81°05'E), Beaver Valley (44°25'N, 80°30'E), and Milton (43°30'N, 79°50'E). We sampled bolt-protected climbing routes rated 5.10–5.14 in difficulty to reflect trends in the development of new climbing routes. We sampled from May through August 2003 to coincide with the flowering season of the vascular plants.

Sampling Design

Within each of the three regions, we classified all accessible cliff faces as either pristine or climbed (i.e., sport climbed). Inaccessible cliffs were those we were not granted permission to sample or those that were >2 hours of hiking time away from the road. We defined climbed cliff faces as those that contained at least one climbing route that was bolt protected, rated 5.10–5.14 in difficulty, and listed in a guidebook or online guide as available for sport climbing for at least 7 years (i.e., equipped with bolts before 1997). On these cliff faces, we randomly sampled two climbing-route transects for each of the four difficulty classes (5.10, 5.11, 5.12, 5.13/14) in each of the three regions, for a total of 24 transects from climbed cliff faces. We defined pristine cliff faces as those that did not fall within the boundaries of any described climbing area and exhibited no evidence of prior climbing disturbance. We sampled 24 randomly selected transects from pristine cliff faces (8 in each of the three regions). We made no attempt to select these transects to match the specific microtopography of the climbed transects; rather, we randomly selected from the pool of microtopographies naturally found across cliffs. All transects, however, met the following minimum criteria: cliff height was between 13 and

28 m, cliff faces were vertical to overhanging, and transects had continuous cliff face extending an additional 2 m on either side.

Within each transect, we placed three 1 × 2 m rectangular quadrats, subdivided into 18, 33.3 × 33.3 cm sub-quadrats, such that the plots extended vertically down the cliff face: top, extending down 2 m directly from the cliff edge; middle, in the middle of the cliff face as measured from the cliff edge to the talus; and bottom, beginning 1 m up from the talus and extending up the cliff face (Fig. 1). On nine of the climbed transects we sampled an additional fourth anchor quadrat because the climbing anchor bolts (which end the climbing route) were located below the top quadrat. The anchor quadrat was placed such that the bolts fell in the direct center of the quadrat. Data from the anchor quadrat were used in place of data from the top quadrat in the analyses of climbing disturbance. All climbed transects were located directly on top of the climbing routes, following the bolts in the cliff face. We marked all quadrats on the cliff face with chalk and followed the contours of the rock to ensure an equal 2-m² surface area for each quadrat. This design resulted in 152 quadrats across 20 separate cliff faces.

Because the cliff face is composed of an assemblage of microhabitats restricted in size by the dimensions of the microtopographic features, small patches of vascular

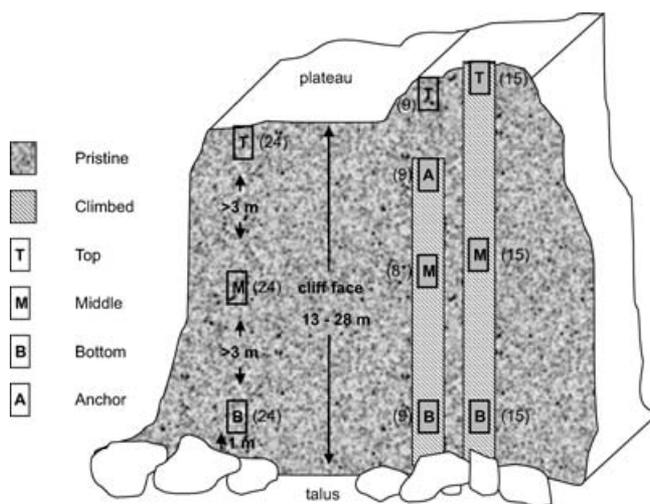


Figure 1. Placement of sampling quadrats on pristine and sport-climbed cliff faces of the Niagara Escarpment showing positioning of top (T), middle (M), bottom (B), and anchor (A) quadrats. The number in parentheses beside each quadrat position reflects the number of replicates for each sample position. Separate climbed anchor and unclimbed top quadrats were sampled for the nine transects where the climbing route finished short of the top of the cliff. An asterisk indicates that the climbing anchors were located in one climbed middle quadrat, so it was classified as an anchor quadrat.

plant, bryophyte, and lichen habitat occur side by side at about the same scale. Thus, a single plot size for all three vegetation groups was considered acceptable. Although other studies of climbing disturbance have used smaller quadrats (e.g., 0.25 m², Nuzzo 1996; 1 m², Rusterholz et al. 2004), we used a larger 2-m² quadrat area in an attempt to reduce variability and to account for the possibility that organisms occur in an aggregated distribution (Krebs 1989).

Vegetation Sampling

We sampled each quadrat for the species richness, vegetation abundance, and community composition of vascular plants, bryophytes, and lichens. Species richness was computed as the number of species found per quadrat. Identification to species of all vascular plants rooted in each quadrat was made in the field. Lichen and bryophyte specimens were collected in the field and identified in the laboratory. Nomenclature follows Gleason and Cronquist (1991), Soper and Heimburger (1982), and Voss (1972) for vascular plants; Crum (1983) and Crum and Anderson (1981) for bryophytes; Brodo et al. (2001), Brodo (1998), Wong and Brodo (1992), and Hale (1969) for lichens. We determined the origin (native or alien to Ontario) of each vascular plant species based on Newmaster et al. (1998) and calculated percent alien vascular plant species richness as the number of alien species divided by the total number of plant species within each quadrat. We calculated the abundance of vascular plants, bryophytes, and lichens for each quadrat as the percentage of subquadrats within the 2-m² quadrat (percent frequency) that contained any vascular plant, bryophyte, or lichen. The community composition of a quadrat was calculated using the abundance (percent frequency) value for each vascular plant, bryophyte, and lichen species in that quadrat. For each species we also calculated its overall frequency on climbed and pristine cliffs as the percentage of climbed or pristine quadrats that contained that species.

Physical Measurements

To assess the physical variables that best reflected differences in cliff-face vegetation community structure, we classified each quadrat based on the presence of climbing (pristine or climbed) and geographic region (Bruce Peninsula, Beaver Valley, or Milton), ranked each quadrat based on latitude, and measured differences in microtopography and factors influencing microclimate. Because the relative importance of various local- and fine-scale physical variables was unknown, we collected data dealing with as many aspects of the physical environment as possible. Local physical factors included (1) cliff height (to the nearest 0.5 m), obtained by lowering a weighted rope marked in 1-m increments from the cliff edge to the talus; (2) transect slope, determined by dividing the height of the cliff face by the distance the top of the

cliff face extended out from the base (i.e., rise over run); (3) aspect, which was decomposed into two linear components, north-south and east-west (Roberts 1986); (4) canopy cover, obtained by adding two values, “percent cover up” and “percent cover out,” which were estimates of the canopy cover in a vertical projection above the quadrat and in a horizontal projection away from the cliff face, respectively; and (5) quadrat position. The brittleness or stability of the rock face was not evaluated because we did not sample unstable rock faces owing to the danger involved.

Individual microtopographic features of the rock face were then counted and measured within each quadrat. Quantified features included ledges, any features extending out horizontally from the face; crevices, narrow, usually linear features (cracks) extending into the face; and solution pockets (hereafter referred to as pockets), circular or ovoid features extending into the face. We determined eight measures of microtopographic heterogeneity for each quadrat: the first four were (1) ledge frequency, (2) crevice frequency, (3) pocket frequency, and (4) total feature frequency. We measured the length and maximum width of each ledge; the length, maximum width, and maximum depth of each crevice; and the diameter and depth of each pocket to the nearest 1mm with a ruler, flexible measuring tape, or rigid metal rod marked in millimeter increments to calculate (5) mean ledge area; (6) mean crevice volume; and (7) mean pocket volume per quadrat. If a feature extended beyond the quadrat, we measured only that portion of the feature within the quadrat boundary. Finally, we computed an estimate of the (8) maximum total volume of soil per quadrat by multiplying the area of each feature covered by soil by the depth of soil at its deepest point (for each feature independently) and summing these volumes. We also determined the presence or absence of vascular plants, bryophytes, and lichens for each feature (ledge, crevice, and pocket) within the quadrat and that individual feature's area (for ledges) or volume (for crevices and pockets).

Statistical Analyses

We performed two-tailed *t* tests to determine whether significant differences ($\alpha = 0.05$) in vascular plant, bryophyte, or lichen species richness existed between pristine and climbed cliff faces. Chi-square tests were performed to determine whether significant differences ($\alpha = 0.05$) in overall frequency existed for each vascular plant, bryophyte, or lichen species between pristine and climbed cliff faces. We used detrended correspondence analysis (DCA) to explore patterns in community composition across pristine and climbed cliff faces. Data from 143 quadrats (72 pristine, 71 climbed) were used in the analyses.

We used stepwise multiple linear regressions to attribute variation in seven response variables: vascular plant

species richness and abundance; bryophyte species richness and abundance; lichen species richness and abundance; and the proportion of alien vascular plant species to differences in geographic region, climbing disturbance, and local- and fine-scale physical factors of the cliff faces. We averaged quadrat values for lichen and bryophyte abundance over transects to achieve normality of errors. Physical factors significant at $\alpha = 0.15$ were included in the overall regression models. Partial r^2 statistics were generated for all physical factors significant at $\alpha = 0.05$. We applied a Bonferroni correction factor to account for testing the seven response variables with the same data set of physical factors ($\alpha = 0.05/7 = 0.0071$).

We used canonical correspondence analysis (CCA) to examine the proportion of the variation in community composition that could be accounted for by regional geography, presence of climbing, and measured physical factors altogether and the relative importance of these variables. We then used partial CCA to examine the proportion of variation in community composition that could be accounted for by regional geography, local physical factors, microtopographic factors, and the presence of climbing individually after factors in the three other categories were defined as covariables.

We used analysis of variance (ANOVA) to determine whether significant differences in ledge frequency, mean ledge size, crevice frequency, mean crevice size, pocket frequency, mean pocket size, total feature frequency, or total volume of soil existed between pristine and climbed quadrats. Quadrat position was included in the model as a blocking factor. We applied a Bonferroni correction factor to account for the number of simultaneous tests performed ($\alpha = 0.05/8 = 0.0065$). A stepwise multiple linear regression was performed to attribute variation in total volume of soil to differences in microtopographic factors and disturbance regime. We used ANOVA to determine whether significant differences in feature size or volume of soil existed among quadrats included (bottom, middle, and anchor) and excluded (top) by climbers in climbing routes. Preplanned contrasts between unclimbed top (+3) and climbed anchor, middle, and bottom (−1, −1, −1) quadrats were performed. Data from the 27 climbed and 9 unclimbed quadrats from the nine climbed transects containing separate anchor and top quadrats were used in the analysis.

We used ANOVA to test for differences in microtopographic feature size (ledge area, crevice volume, and pocket volume) between pristine and climbed cliff faces for features that did not support vascular plants, bryophytes, or lichens to determine whether climbers were removing vegetation from features that were large enough to support vegetation in the absence of climbing. We used ANOVA to test for differences in microtopographic feature size between pristine and climbed cliff faces for features that supported vascular plants, bryophytes, and lichens to determine whether features large enough to support

vegetation on pristine cliff faces also supported this vegetation with climbing present. Results were considered significant at $\alpha = 0.017$ (reflecting a Bonferroni correction factor of 3).

In all analyses, we transformed data where necessary to meet assumptions of parametric analyses. Sampling date was used as a covariate in all analyses. We performed all univariate analyses in SAS (version 8.2, SAS Institute 2001) and all multivariate analyses in CANOCO (version 4.5, ter Braak & Smilauer 2003).

Results

Differences in Vegetation between Pristine and Climbed Cliffs

We found 134 different taxa (53 vascular plant species, 23 bryophyte species, and 58 lichen taxa) across all cliff faces (both pristine and climbed) we sampled. Pristine cliff faces had nearly twice the vascular plant richness of climbed faces (1.9 vs. 1.1, $p = 0.028$). Species richness of bryophytes was also one-third lower on climbed cliff faces when compared with pristine, but this difference was not statistically significant (0.43 vs. 0.65, $p = 0.227$). Lichen species richness was nearly identical across pristine and climbed cliff faces (6.65 vs. 6.88, $p = 0.680$). Forty of the 134 taxa found across all sampled cliff faces were found in more than 5% of quadrats on either pristine or climbed cliff faces, although only 7 of these taxa were vascular plant species and only 5 were bryophyte species, with the remainder of taxa represented by lichens. Within the 40 common species, 10 taxa had significantly greater frequencies on pristine cliff faces (2 vascular plant species, 2 bryophyte species, and 6 lichen taxa) and 10 taxa had significantly greater frequencies on climbed cliff faces (similarly, 2 vascular plant species, 2 bryophyte species, and 6 lichen taxa) (Table 1). Vascular plant species with significantly greater frequencies on pristine cliff faces were the native tree species eastern white cedar (*Thuja occidentalis* L.) and a naturalized herbaceous alien, herb-robert (*Geranium robertianum* L.). The natives, fragile fern (*Cystopteris fragilis* [L.] Bernh.) and smooth cliff-brake (*Pellaea glabella* Mett. ex Kuhn spp.) occurred more on climbed cliff faces. Fragile lichens such as the foliose *Leparia lobificans* Nyl. and squamulose *Acarospora glaucocarpa* (Ach.) Korb occurred significantly more on pristine cliff faces.

When examining the location of individual species in DCA ordination space, a separation of vegetation groups occurred along axis 1, with bryophyte species located toward the left in ordination space, vascular plant species located toward the right, and lichen species filling the remainder of the ordination space (Fig. 2). There was no separation of climbed from pristine quadrats when the location of quadrats in ordination space was layered on the species ordination, indicating that climbed sites have

not diverged toward a separate community of species. Instead, climbed quadrats appeared to support a subset of the flora found on pristine cliff faces.

Microsite Factors versus Climbing Disturbance to Cliff Vegetation

When microtopographic differences between sites were included in our analysis, neither species richness nor abundance of cliff-face vascular plants, bryophytes, and lichens decreased as a direct result of the presence of climbing (Table 2). Instead, species richness and abundance of all three vegetation groups were closely related to microtopographic feature size and frequency and factors affecting microclimate such as quadrat position and aspect (Table 2). In particular, species richness or abundance for all three vegetation groups was correlated with differences in soil volume, with vascular plant richness and abundance increasing with increasing volumes of soil and bryophyte richness and lichen abundance increasing with decreasing volumes of soil.

The CCA eigenvalues for axes 1 and 2 were high for vascular plants and bryophytes compared with those from the DCA, indicating that most of the variation between quadrats could be accounted for by the environmental variables we chose (Table 3). The CCA eigenvalues were lower for lichens, indicating that environmental variables other than those we measured are responsible for at least some of the variability in species composition among quadrats. Quadrats were separated from one another in the CCA ordination space based on geographic region, although many local- and fine-scale physical factors showed strong correlations with the different geographic regions (Fig. 3). A clustering of climbed sites toward the left, along axis 1, pulled the climbed centroid away from the center, indicating a difference in the community of species on climbed cliffs. Climbed sites, however, were also strongly correlated with decreased mean ledge area, decreased soil volume, and decreased canopy cover. When partial CCA was run to remove potentially covarying microtopographic and local physical factors, the presence of climbing was the factor that least explained variation in community composition for every vegetation group (Table 3).

Climber Selection of Specific Microtopography

A total of 2971 individual microtopographic features were identified within the sample area, with 1550 features on pristine cliff faces and 1421 on climbed cliff faces. Pristine cliff faces averaged more crevices and ledges per quadrat compared with cliff faces selected for advanced sport-climbing routes, and individual crevices were greater in volume and individual ledges were larger in area on pristine than on climbed cliff faces, although not all differences were statistically significant (Table 4). Climbed cliffs had greater numbers of pockets of a larger mean

Table 1. Percent frequencies of the 40 common^a species on pristine and climbed cliff faces of the Niagara Escarpment in southern Ontario, Canada.

Species ^b	Frequency		Difference	p ^d
	pristine (%) ^c	climbed (%) ^c		
Vascular plants				
pristine				
<i>Thuja occidentalis</i> L.	25	7	18	<0.0001
<i>Geranium robertianum</i> L.	14	1	13	0.0003
<i>Campanula rotundifolia</i> L.	6	1	5	
<i>Cystopteris bulbifera</i> (L.) Bernh.	18	14	4	
climbed				
<i>Pellaea glabella</i> Mett. ex Kuhn spp.	18	37	19	<0.0001
<i>Cystopteris fragilis</i> (L.) Bernh.	7	14	7	0.0050
<i>Poa compressa</i> L.	19	20	1	
Bryophytes				
pristine				
<i>Tortella tortuosa</i> (Hedw.) Limpr.	6	0	6	0.0153
<i>Orthotrichum anomalum</i> Hedw.	7	1	6	0.0294
<i>Gymnostomum recurvirostrum</i> Hedw.	11	8	3	
climbed				
<i>Gymnostomum aeruginosum</i> Sm.	6	13	7	0.0019
<i>Bryum lisae</i> var. <i>cuspidatum</i> (B.S.G.) Marg.	4	8	4	0.0320
Lichens				
pristine				
<i>Lepraria lobificans</i> Nyl.	35	17	18	0.0002
<i>Lecania nylanderiana</i> A. Massal.	18	1	17	<0.0001
<i>Acarospora glaucocarpa</i> (Wahlenb. ex Ach.) Körber	36	24	12	0.0113
<i>Caloplaca citrina</i> (Hoffm.) Th. Fr.	65	56	9	
<i>Catillaria lenticularis</i> (Ach.) Th. Fr.	8	0	8	0.0026
sterile white crust ^e				
<i>Psorotichia schaeferi</i> (A. Massal.) Arn.	7	0	7	0.0063
<i>Collema fuscovirens</i> (With.) Laundon	21	14	7	
<i>Verrucaria</i> sp. ^f	17	11	6	0.0003
<i>Protoblastenia rupestris</i> (Scop.) Steiner	15	10	5	
<i>Bacidia granosa</i> (Tuck.) Zahlbr.	7	3	4	
<i>Caloplaca velana</i> (A. Massal.) Du Rietz	10	6	4	
<i>Caloplaca</i> sp. ^g	15	11	4	
<i>Lecania perproxima</i> (Nyl.) Zahlbr.	6	4	2	
climbed				
<i>Caloplaca cirrochroa</i> (Ach.) Th. Fr.	50	73	23	<0.0001
<i>Caloplaca feracissima</i> H. Magn.	33	55	22	
<i>Lecanora perpruinosa</i> Fröberg	11	28	17	<0.0001
<i>Lecidella stigmatea</i> (Ach.) Hertel & Leuck.	11	27	16	<0.0001
<i>Lecanora dispersa</i> (Pers.) Sommerf.	32	44	12	0.0120
<i>Aspicilia contorta</i> (Hoffm.) Kremp.	3	13	10	<0.0001
<i>Caloplaca flavovirescens</i> (Wulfen) Dalla Torre & Sarnth.	25	31	6	
<i>Candelariella aurella</i> (Hoffm.) Zahlbr.	11	17	6	
<i>Phaeophyscia hirtella</i> Essl.	1	6	5	0.0003
<i>Rhizocarpon hochstetteri</i> (Körb.) Vain.	1	6	5	
<i>Buellia alboatra</i> (Hoffm.) Th. Fr.	11	15	4	
<i>Lecanora crenulata</i> Hook.	38	41	3	
no difference				
<i>Acrocordia conoidea</i> (Fr.) Körber	14	14	-	
Sterile brown crust ^b				
	56	56	-	

^aPresent in at least 5% of pristine or climbed quadrats.

^bSpecies are listed under the disturbance category (pristine or climbed) where they were more frequent and based on the magnitude of the difference in frequency between disturbance categories.

^cPercentage of quadrats in which each species was present.

^dSignificant differences between disturbance categories determined by chi-square tests; only significant values at $p < 0.05$ are listed.

^eWithout apothecia, with or without diffuse soralia or soredia; genus unknown.

^fWith apothecia and thallus, spores one celled, ellipsoid; may include *V. calkinsiana*, *V. fuscilla*, *V. muralis*, *V. nigrescens*, and possibly others.

^gWith apothecia and poorly developed thallus; may include *C. feracissima*, *C. holocarpa*, *C. cf. dalmatica*, *C. flavovirescens*, *C. velana*, and possibly others.

^hWithout apothecia, soralia, or soredia; probably includes *Verrucaria* sp., *Lecania* sp., *Bacidia* sp., *Catillaria* sp. and others.

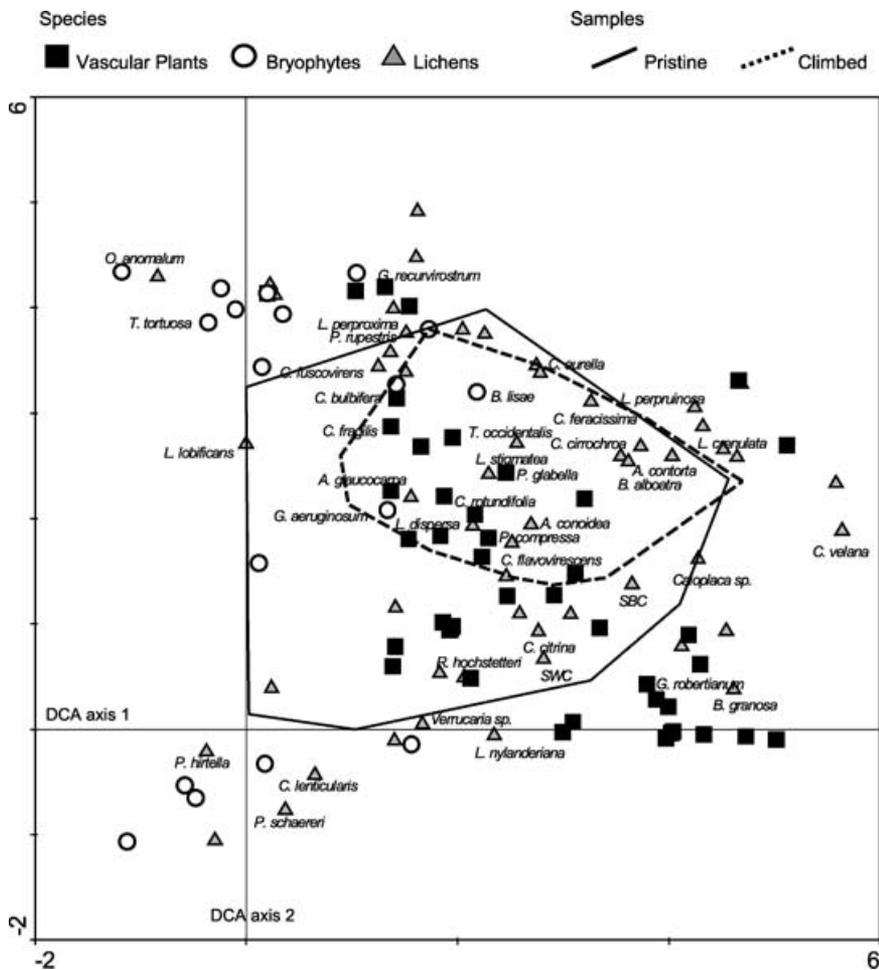


Figure 2. Ordination diagram of vascular plant, bryophyte, and lichen species produced by detrended correspondence analysis of species frequencies on the Niagara Escarpment, Ontario, Canada ($\lambda_1 = 0.579$, $\lambda_2 = 0.542$). Geometric shapes represent ordination of pristine and climbed quadrats. Named symbols represent the 40 most common taxa (see Table 1; SBC, sterile brown crust; SWC, sterile white crust).

size than pristine cliffs. Overall, total available microtopographic feature area per quadrat was a function of both the number and mean size of crevices, ledges, and pockets. Climbed cliff faces had one-third less crevice volume and >50% less ledge area per quadrat than pristine cliff faces. Climbed quadrats supported only 10% of the soil volume of pristine quadrats (Table 4). Regression results indicated that differences in soil volume were related mainly to differences in microtopography, with soil volume decreasing with decreasing ledge area (partial $r^2 = 0.47$, $p < 0.0001$, $n = 143$) and decreasing numbers of crevices (partial $r^2 = 0.05$, $p = 0.0015$, $n = 143$) and pockets (partial $r^2 = 0.03$, $p = 0.013$, $n = 143$). Climbing presence also decreased soil volume (partial $r^2 = 0.03$, $p = 0.023$, $n = 143$), although the actual proportion of variation explained by climbing was small (3%) compared with that of microtopography (55%).

In 9 of the 24 climbing routes sampled (38%), climbing anchors were placed >3 m down the face from the edge of the cliff, indicating the route developer's choice to end the route well below the top of the cliff despite total cliff height falling within standard climbing route lengths. When comparing the microtopography of plots falling within the climbing route (bottom, middle, and anchor)

to that of plots excluded from the route but still falling in the same transect (top), differences in feature size were highly significant, indicating climber selection for specific feature sizes. Top quadrats had significantly larger ledges ($F_{1,27} = 12.46$, $p = 0.001$) and crevices ($F_{1,25} = 5.01$, $p = 0.034$). Top quadrats also contained greater volumes of soil ($F_{1,27} = 22.27$, $p < 0.0001$) than quadrats included in the climbing route. Total soil volume was almost 4 times greater on these quadrats than on the next closest quadrat position below them and more than 13 times greater than the average total soil volume across all quadrats included in the climbing route.

Climber Removal of Vegetation

If sport climbing is resulting in the removal of vegetation from features previously supporting it, one would expect to see an increase in the mean size of features not supporting vegetation on climbed cliffs compared with pristine cliffs. Results of preplanned contrasts on analyses of variance indicated that crevices, ledges, and pockets not supporting vascular plants and bryophytes were not significantly larger on climbed cliff faces compared with pristine (all $p > 0.05$). The mean size of ledges, crevices,

Table 2. Test statistics, correlation coefficients, and significance levels obtained from stepwise, linear multiple regression models for seven response-to-climbing variables of the vegetation community on cliff faces of the Niagara Escarpment, Ontario, Canada.

Response variable	df	F	R ² (adjusted)	p	Physical factors ^a	Sign	Partial r ²	p ^b	
Richness	vascular plant	5,131	18.04	<0.0001	quadrat position (height)	+	0.23	<0.0001***	
					volume of soil	+	0.09	<0.0001***	
					pocket frequency	+	0.04	0.0040*	
					crevice volume	-	0.03	0.0132	
	bryophyte	5,40	6.68	0.455	0.0001	crevice frequency	+	0.02	0.0487
						crevice volume	+	0.16	0.0054**
						volume of soil	-	0.11	0.0087*
	lichen	6,136	15.50	0.417	<0.0001	ledge area	+	0.10	0.0185
						pocket frequency	+	0.21	<0.0001***
						aspect—northness	+	0.11	<0.0001***
quadrat position (height)						+	0.05	0.0020*	
crevice frequency						+	0.03	0.0293	
Abundance	vascular plant	5,131	12.00	<0.0001	climbing presence	+	0.02	0.0487	
					pocket frequency	+	0.18	<0.0001***	
					quadrat position (height)	+	0.07	0.0004**	
	bryophyte	4,41	3.20	0.238	0.0225	volume of soil	+	0.02	0.0402
						total feature frequency	+	0.07	0.0438
	lichen	5,40	9.92	0.554	<0.0001	quadrat position (height)	+	0.24	0.0005**
						ledge frequency	+	0.14	0.0038*
						climbing presence	+	0.11	0.0044*
						volume of soil	-	0.04	0.0500
						latitude (region)	-	0.17	<0.0001***
	Alien plant species (%)	4,79	9.29	0.320	<0.0001	ledge area	+	0.08	0.0032*
						crevice frequency	+	0.04	0.0462

^aIndividual physical factors increasing or decreasing the response variable as indicated by sign.

^bAsterisks indicate individual factor significance after applying a Bonferroni correction: *p < 0.0071; **p < 0.0014; ***p < 0.00014).

and pockets supporting vascular plants and bryophytes also did not differ significantly between pristine and sport-climbed cliff faces (all $p > 0.05$). This indicates that features large enough to support vegetation in the absence of disturbance continue to support this vegetation with a climbing disturbance present. As well, no significant differences existed in terms of crevice or pocket volumes among features supporting and not supporting lichens across pristine and climbed cliff faces (all $p > 0.05$).

Discussion

Comparative studies in ecology present a tremendous number of challenges because one is observing complex systems after events have taken place without a clear picture of what existed previously. We solved several design problems in prior comparative studies of climbing disturbance by selecting climbing routes consistent with recent trends in the sport and by evaluating the relative importance of climbing disturbance and the microsite characteristics of the cliff face to the organization of cliff-face vegetation communities.

We started off examining vegetation patterns across pristine and climbed cliffs, knowing that these two classes

of sites were qualitatively unequal in their microtopography. As in most previous research on climbing impact on cliff vegetation, climbed cliff faces supported a lower mean species richness of vascular plants and bryophytes and significantly different frequencies of individual species when compared to pristine cliff faces when microsite differences between cliffs were not controlled. When we evaluated the relative contribution of the presence of climbing versus other physical factors to the divergence in vegetation patterns across these cliffs, however, our results revealed that vegetation differences were not directly related to climbing disturbance; rather, they reflected microsite differences between cliffs selected by climbers and the remaining pristine cliff faces.

Our results agreed with Nuzzo's (1996), who found that physical factors other than climbing disturbance can influence vascular vegetation, and confirm Farris' (1998) hypothesis that differences in vegetation between pristine and climbed cliffs may result from climbers avoiding the more heavily vegetated cliffs because of the presence of the vegetation itself or the geological structure of the area. Our results for bryophytes are consistent with Studlar's (1983) finding that the growth rates and survival of different bryophyte species are affected by microtopography, litter levels, and competition from other bryophytes and vascular plants.

Table 3. Eigenvalues for the first two axes of each ordination conducted to show the relative influence of climbing presence, regional geography, local physical factors, and microtopographic factors on the species composition of vascular plants, bryophytes, and lichens on cliff faces of the Niagara Escarpment, Ontario, Canada.

Species group	Analysis type ^a	Eigenvalues	
		axis 1	axis 2
Vascular plants	DCA	0.818	0.569
	CCA (all variables)	0.611	0.498
	partial CCA, microtopography	0.378	0.270
	partial CCA, regional geography	0.299	0.116
	partial CCA, local physical factors	0.262	0.241
	partial CCA, climbing presence ^b	0.159	
Bryophytes	DCA	0.978	0.713
	CCA	0.852	0.787
	partial CCA, microtopography	0.520	0.320
	partial CCA, local physical factors	0.433	0.305
	partial CCA, regional geography	0.222	0.067
	partial CCA, climbing presence ^b	0.212	
Lichens	DCA	0.497	0.400
	CCA	0.274	0.221
	partial CCA, local physical factors	0.160	0.113
	partial CCA, regional geography	0.154	0.079
	partial CCA, microtopography	0.141	0.120
	partial CCA, climbing presence ^b	0.102	

^aAbbreviations: DCA, detrended correspondence analysis; CCA, canonical correspondence analysis.

^bOnly one axis could be created because of the single constraining variable.

Our results disagree with the results of Müller et al. (2004) that proximity to climbing has a significant influence on cliff-face vegetation after differences in rock fracturing are accounted for. This inconsistency might be explained by their ranking of rock fracturing not completely capturing the microtopographic variability between pristine and climbed cliffs. In other studies of climbing impact, microtopographic variability between disturbance categories was not measured (Herter 1996; Kelly & Larson 1997; Camp & Knight 1998; McMillan & Larson 2002; Rusterholz et al. 2004). Thus, differences in vascular plant or bryophyte richness, abundance, or cover between pristine and climbed cliffs in these studies may in fact be reflecting small microsite differences among sites and not disturbance by climbers.

We found no shifts in vascular plant community composition between pristine and sport-climbed cliff faces. Rather, sport climbers selected areas that supported a distinct subpopulation of all vascular plant species present on pristine cliff faces. Increases in the abundance of native ferns and decreases in the abundance of eastern white cedar and herb-robert were observed on climbed faces. These results are consistent with trends observed by Rusterholz et al. (2004), who found that the density of forbs and shrubs is reduced and the density of ferns tends to increase in climbed areas compared with unclimbed controls. McMillan and Larson (2002) found that climbed cliff faces support greater proportions of alien species

compared with pristine cliff faces (although not significantly so). In our study the proportion of alien species did not increase with climbing disturbance; instead, it increased with increasing ledge size and crevice frequency and was highly correlated with the Milton region, where disturbance from dust and pollutants from active quarry operations are present.

We found no significant differences in lichen richness between pristine and climbed cliff faces across the Niagara Escarpment, agreeing with results from McMillan and Larson (2002). Reductions in the frequency of a common foliose species (*L. lobificans*) and a common squamulose species (*A. glaucocarpa*) and increases in the frequency of the crustose *Caloplaca* and *Lecanora* species were evident, however, on climbed cliffs compared with pristine cliffs. Niche overlap is evident between lichens and climbers because lichens occur on smaller, soil-free features on cliff faces (Kuntz 2004) and climbers also selected for these features when establishing climbing routes. Despite this overlap, local and small-scale physical factors of the cliff face were better able to explain variation in lichen community composition than climbing disturbance. Both Nuzzo (1996) and Farris (1998) found reductions in lichen cover on climbed cliffs compared with unclimbed controls. These researchers used photographic techniques to determine lichen cover (rather than field sampling), however, and their values for the cover of crustose species may be underestimates because crustose lichens are cryptic and often only apothecia are visible (even with a hand lens). We found the majority of lichens on climbed cliff faces were crustose; therefore, discrepancies in results may simply reflect differences in the ability of a sampling technique to detect these lichens.

Conclusions and Management Implications

The differentiation of vegetation across cliff faces is highly correlated with local- and fine-scale physical factors of the cliff face (Kuntz 2004). Our results revealed that advanced sport climbers select areas of the cliff face with specific microsite characteristics and indirectly select sites that support a subset of the vegetation community found on pristine cliff faces. Differences in the presence, richness, abundance, and community composition of cliff-face vegetation between climbed and pristine sites are not resulting from a direct disturbance by advanced sport climbers.

Management recommendations to restrict the development of new climbing routes based on the interpretation of results from prior studies on impacts of climbing (i.e., reductions in vegetation richness, abundance, and cover are a direct result of climbing disturbance) must be weighed against this new evidence. Different conclusions regarding impacts of climbing may occur, however, should one examine climbing routes of beginner and moderate difficulty levels. These climbing routes may have microsites large enough to support vegetation that

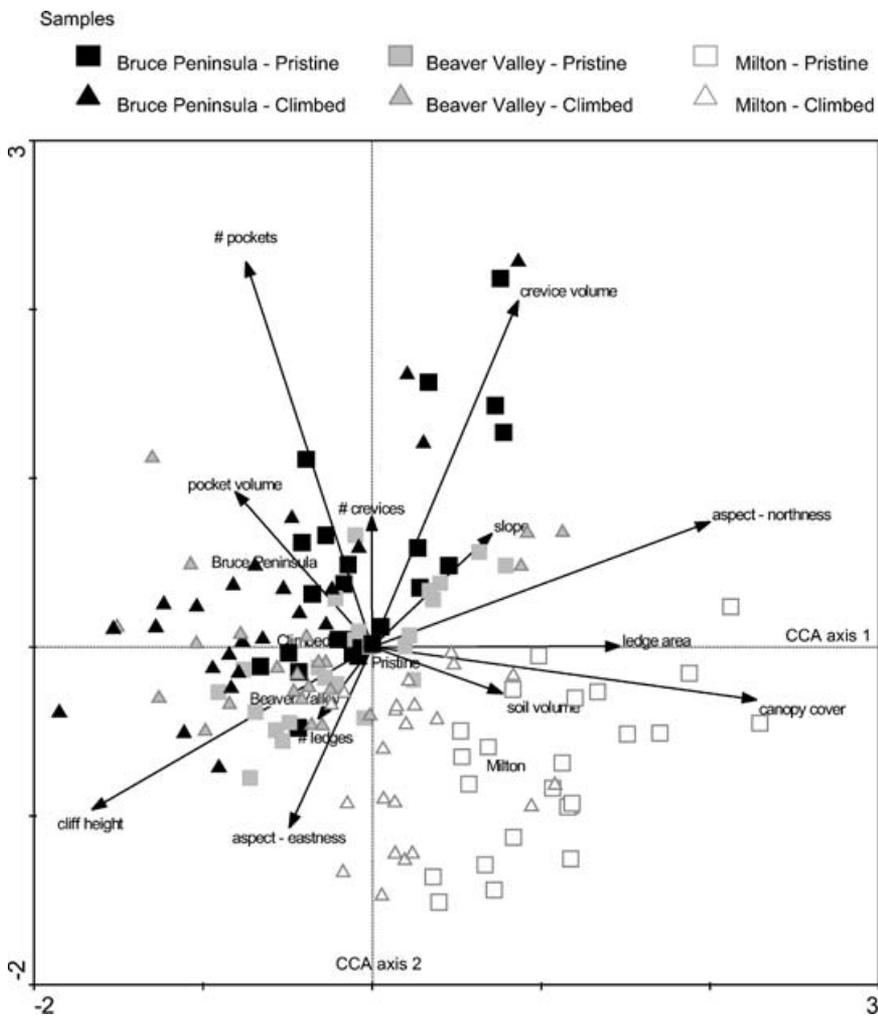


Figure 3. Ordination diagram produced by canonical correspondence analysis of vascular plant, bryophyte, and lichen species frequencies on the Niagara Escarpment, Ontario, Canada ($\lambda_1 = 0.318, \lambda_2 = 0.276$). Vectors indicate the direction in which each of the physical factors separate the data points. The length of the vector indicates the relative importance of the factor in its influence over community composition. Nominal physical variables (geographic regions and climbing presence) are shown with their names as centroids.

may be damaged by trampling and may also see greater traffic than the more difficult climbing routes. Additionally, the potential disturbance of vegetation on cliff faces by sport climbers on the Niagara Escarpment may not yet be measurable. The effects of sport climbing may not be apparent until after 7-12 years of use. Data on usage of climbing routes of specific difficulty levels would

contribute greatly to our understanding of climbing disturbance and should be incorporated into future studies.

We did not quantify measures of climbing disturbance such as limb removal, bark abrasion, reductions in average leaf or flower number or size, or differences in growth rate, colony size, or reproductive rate. Thus, land managers with concerns regarding a specific rare species

Table 4. Raw mean values, test statistics, and significance values for microtopographic feature frequency, mean feature sizes, and volume of soil per quadrat obtained from blocked analysis of variance tests (fixed: disturbance category; quadrat position) on unclimbed (pristine) and climbed cliff faces of the Niagara Escarpment, Ontario, Canada.^a

Physical factor	Raw mean values		F	df	p ^b
	pristine	climbed			
Ledge frequency	9.3	7.6	3.83	1,139	0.0524
Crevice frequency	7.3	4.6	17.02	1,139	<0.0001***
Pocket frequency	4.5	5.2	0.57	1,139	0.4516
Mean ledge size (cm ²)	392	164	9.16	1,137	0.0050*
Mean crevice volume (cm ³)	3786	2625	2.08	1,139	0.1512
Mean pocket volume (cm ³)	213	267	0.09	1,94	0.7648
Total feature frequency	21.1	17.4	9.48	1,139	0.0047*
Total volume of soil (m ³)	0.0186	0.0020	16.39	1,101	0.0001***

^aSignificance is after a Bonferroni correction.

^bSignificance: *p < 0.00625, **p < 0.00125, ***p < 0.000125.

should consider further study on the potential impacts of climbing on that species. As well, impacts of climbing are not restricted to the cliff face. Climbers must access cliff faces from either the plateau above or the talus below. Both McMillan and Larson (2002) and Müller et al. (2004) investigated the impacts of climbing on talus plant communities and found more severe trampling impacts on the talus of climbed cliffs than on talus of unclimbed cliffs. Finally, impacts of climbing are not restricted to cliff vegetation. Significant negative effects of rock climbing also have been reported for rock-dwelling gastropods (McMillan et al. 2003).

Based on our results, we recommend the creation of a policy that allows sport climbers to establish new climbing routes at difficulty levels of 5.10 and above. Such a policy will receive more compliance than blanket restrictions on all new development of climbing routes. We do not recommend the establishment of new routes of <5.10 difficulty because research has not been done to determine whether these routes overlap with cliff-face microsites where sensitive vegetation may be disturbed.

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